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T H E S I S

THE STATUS OF THE PROBLEM OF THE TRANSMISSION OF ACQUIRED CHARACTERS

by

Horace Joffre Prescod

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THE STATUS OF THE PROBLEM OF THE TRANSMISSION OF ACQUIRED CHARACTERS

INTRODUCTION

The belief that a bodily modification is inherited is not only ancient, but has also been a matter of bitter controversy. The question still remains unsolved, but the weight of both contemporary opinion and proof is against it. Much has been written on both sides and the question has seemed to be as interminable as free will versus determinism, as recurrent as the ocean tides, as perennial as the winter's snows, and seemingly as eternal as the universe. The believers of either principle have been firmly convinced of the correctness of their position, and therefore discussions have often been characterized by a spirit of reprehensible dogmatism and much heat but little light has been emitted. Eminent scientists have come out strongly in favor of either position and no matter which side we take, we find ourselves in distinguished company. Therefore, a fair and impartial appraisal of each view in the light of recent experimental data as we can conveniently compress into a brief paper will be made. Time and space preclude an exhaustive examination of all relevant data.

The whole question has more than a purely academic interest. The human race exerts a marked control over its environment, and that of other organisms. Granting intelligent

direction and constant application of a given influence, can the two factors act together, or must they forever remain separate, the one all powerful, the other impotent? Can man expect as a result of the many things he does for himself, an environment in his remote descendants, or must their inheritance be determined by some unknown force working on the germ plasm? These and similar questions engage the attention of educators, physicians, and sociologists. In a broad sense, however, the problem is one evolutionary theory.

The inheritance of an acquired character means:

1-The production of a definitely new somatic character by a change in environment or functional activity, and

2-The new character must reappear in the offspring at least in part after the removal of the original stimulus.

PART I

THE ANTIQUITY OF THE PROBLEM

In a discussion of the transmission of acquired characters, one wonders where to begin since the problem is as old as antiquity itself. Hence it may be well to present a brief sketch of the history of this problem during the ages. Most classical and mediaeval naturalists believed that acquired characters were inherited. From 400 B. C. to the 19th century this doctrine was accepted without question. Thus the Lamarckian doctrine is but the restatement of classical beliefs.

Hippocrates, probably was the first to describe pangenesis. "For the seed comes from all parts of the body, healthy seed from healthy parts, diseased seed from diseased parts."[1] He used this belief to explain how somatic changes could be inherited.

Democrates agreed with this viewpoint, but Aristotle refused to accept it, and classical authority was thus divided into two distinct schools with the Galenic literature and some of the Christian fathers supporting Hippocrates.

The 13th century witnessed a great deal of speculation on the mechanism of heredity. Roger Bacon (1268) explained the decreasing life span of man on the basis of the transmission of acquired characters. St. Thomas Aquinas (1256) in his "Summa

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1-Zirkle, Conway, Further notes on Pangenesis and the Inheritance of Acquired Characters, Amer. Nat., Vol. 70, p. 529-30

Theologica" explained the inheritance of acquired characters in the following manner:

"...thus a leper may beget a leper, or a gouty man may be the father of a gouty son, on account of some seminal corruption, although this corruption is not leprosy or gout...

"But all these explanations are insufficient. Because, granted that some bodily defects are transmitted by way of origin from parent to child, and granted that even some defects of the soul are transmitted in consequence, on account of a defect in the bodily habit, as in the case of idiots begetting idiots; nevertheless the fact of having a defect, by way of origin seems to exclude the notion of guilt, which is essentially something voluntary."[1]

Jacob Rueff (1554) discussed the origin of semen as proof of the transmission of acquired characters in his "De Conceptu & Generatione Hominis."

"...For, if we should say that the semen is produced in only one or another part (of the body), anyone will see that this follows by correct reasoning - (namely) that only those same parts should be reproduced. And so, we can rightly say, that in addition to what originates in the brain the semen is produced from the whole body and from all the most important parts thereof; indeed, its effect instructs us as to its cause (origin), especially since in the offspring we see the distinct members perfectly completed to the exact form of the

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1-Zirkle, op. cit., p. 531.

body. Also, against the opinions of others, we have on our side Hippocrates himself, easily the greatest of all physicians; who himself asserted that the seed was gathered from the whole body, and so I say that what is begotten corresponds to the constitution of the begetter - a weak man being born from weak semen and a strong man from strong seed. In addition to these arguments comes the fact that we often observe in children those diseases or defective marks of the body which are present in their parents - things which we entirely believe to have passed into them (the children) through a defect of the seed (genitura). And so, having certainly established these facts regarding the origin and material constitution of the genital semen, these things suffice as a preface."[1]

Pierre Belon also used pangenesis as proof of inherited somatic modifications. In his "L'Histoire de la natur des oyseaux" (1555) he argues:

"Just as seeds produce such plants as those from which they have been gathered, so animals starting their growth from the seed of their sex, become at length like to those from which they have originated. The seeds are excrements of the bodies, which have the potentialities of those substances from which they have come, and which proceed from the last digestion of the body's food...But the seed of the female being an excrement also, has as a property all the parts of the body, which are engendered from it - not in present action but merely

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1- Zirkle, op. cit., p. 535.

in mattbr and potienally does it have those parts whereby nature has made the female to be different from the male and hence it happens that sometimes deformed animals engender deformed offspring - at one time, male and another time female."[1]

Seventeenth century records on the transmission of acquired characters are quite numerous. Sir Kenelm Digby's "Immortality of Reasonable Souls" contains a lengthy argument for this belief, based again on pangenesis.

"To deduce this from its origine, we may remember how our Masters tell us, that when any living creature is passed the heat of its augmentation or growing; the superfluous nourishment settleth itself in some appointed place of the body to serve for the production of some other. Now it is evident that this superfluity cometh from all parts of the body, and may be said to contain in it after some sort the perfection of the whole living creature. Be it how it will, it is manifest that the living creature is made of this superfluous moysture of the parent: which, according to the opinion of some, being compounded of severall parts derived from the several limbs of the parent; those parts when they come to be fermented in convenient heat and moisture, do take their posture and situation, according to the posture and disposition of parts that the living creature had from whence they issued: and then they growing daily greater and solider, (the effects of moysture and heat;) ~~and~~ do at the length become such a creature as that was,

1- Zirkle, op. cit., p. 536.

from whence they had their origine."[1]

"Whence it followeth, that if any part be wanting in the body whereof this seed is made, or be superabundant in it; whose virtue is not in the rest of the body, or whose superabundance is not allaid in the rest of the body; the virtue of that part, cannot be in the bloud, or will be too strong in the bloud, and by consequence, it cannot be at all, or it will be too much in the seed. And the effect proceeding from the seed, that is, the young animall will come into the world savouring of that origine; unlesse the mothers seed, do supply or temper what the fathers was defective or superabundant in; or contrariwise the fathers do correct the errours of the mothers..."[2]

Although, Nathaniel Highmore disagreed with Digby's conception of heredity, yet he advocated the transmission of acquired characters in his "History of Generation." After explaining how wrong Digby must have been he concludes:

"Myself also have seen a kinde of Poultry without rumps: which breeding with their own kind still brought forth Chicken wanting that part: if with others, sometimes they had rumps, sometimes but part of a rump. And not long since I saw a Mungril Bitch, that had her tail cut close to her body almost, whose Whelps were half without tails, and half with tails: The next year following, she brought them forth all with long tails, as she had before the cutting off. Which though it seems to favor

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1- Zirkle, op. cit., pp. 538-539.
2- Ibid, pp 540

(as I said) this opinion, it; as may appear by the frequent perfect generations of mutilated creatures; which beget children or issue with two legs or arms though they had but one; Spaigniels, whose tails are always cut, bring forth Whelps whose tails need as much cutting, as their Dams or Sires did. Wee must therefore look out some other way, how this may be done without the parts themselves."[1]

The Eighteenth Century, which witnessed the recrudescence of the theory of Evolution, produced three great naturalists that believed in the transmission of acquired modifications, Buffon, Erasmus Darwin, and Lamarck.

Buffon (1707-88) explained evolution by the direct influence of the environment in the modification of the structures of animals and plants and the conservation of these modifications through heredity. He expressed himself as believing that climate has had a direct effect in the production of various races of man, that new varieties of animals have been formed through human intervention, and that similar results are produced by geographic migration and through isolation.

Erasmus Darwin (1731-1802), grandfather of Charles Darwin, postulated an exceedingly clear principle for the transmission of acquired characters in explaining evolution. "All animals," he said, "undergo transformations which are in part produced by their own exertions, in response to pleasures and pains, and many of these acquired forms or propensities are transmitted to their posterity." And he writes further, in explaining evol-

1- Zirkle, op. cit., p. 541.

ution:

"From thus meditating upon the minute portion of time in which many of the above changes have been produced, would it be too bold to imagine, in the great length of time since the earth began to exist, perhaps millions of ages before the commencement of the history of mankind, that all warm-blooded animals have arisen from one living filament, which the first great Cause imbued with animality, with the power of acquiring new parts, attended with new propensities, directed by irritations, sensations, volitions, and associations, and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down these improvements by generation to posterity, world without end?"[1]

Lamarck (1744-1829), the greatest of French evolutionists, has long been recognized as the founder of the doctrine, the transmission of acquired characters. In his "Philosophie Zoologique," Lamarck expresses his theory of evolution in the form of four laws.

1. "Life, by its proper forces, continually tends to increase the volume of every body which possesses it, and to increase the size of its parts, up to a limit which brings it about."

2. "The production of a new organ in the animal body results from the supervention of a new want which continues to make itself felt, and a new movement which this want gives

1- Newman, H. H., Readings in Evolution, p. 18.

rise to and maintains."

3. "The development of organs and their powers of action are constantly in ratio to the employment of these organs."

4. "Everything which has been acquired, impressed upon, or changed in the organization of individuals during the course of their life is preserved by generation and transmitted to new individuals which have descended from those which have undergone these changes."[1]

It is around this fourth law that the controversy has raged and which remains to this day unsettled. Lamarck is thus credited with being the first to postulate the doctrine in its fullest terms and his name has become an exceedingly common synonym for the doctrine of the inheritance of acquired somatic modifications.

We have thus traced this belief from the days of antiquity to the 19th century. We have seen that it traces back to Hippocrates, and that from the 4th century, B. C. to the 19th, it was accepted as a matter of course. Only two individuals during this period have been noted who did not believe in this doctrine. It reached its fullest expression with Lamarck who used it to explain the formation of new species in the course of evolution.

1-Newman, op. cit., p. 19.

PART II

THE SIGNIFICANCE OF EVOLUTION TO THE PROBLEM

EMBRYOLOGICAL AND PALEONTOLOGICAL EVIDENCE

Let us now turn to evolution and see what bearing it has had on this theory. Lamarck makes the "inheritance of acquired changes" the crucial factor in evolution. He advances proof to illustrate his theory. He refers all rudimentary structures to disuse, such as the embryonic teeth of certain whales, the eyes of the mole, and of the proteus, the blind salamander of the Austrian caves. He said that the organ of hearing has developed everywhere by direct action of vibrations of sound.[1] Again, he explains the development of the webbed feet of birds, by their being attracted to swampy ground and spreading the toes, the skin being thus stretched between them.[2]

His conception of the causal relations of the desires and wants of animals is illustrated thus:

"I conceive that a Gasteropod mollusc, which, as it crawls along, finds the need of touching the bodies in front of it, makes efforts to touch those bodies with some of the foremost parts of the head, and sends to these every time quantities of nervous fluids as well as of other liquids; I conceive and say, that it must result from this reiterated afflux towards the point in question, that the nerves which abut at these points, will by slow degrees be extended. Now, as in the same

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1-Lamarck, J. B., Zoological Philosophy, p. 116.
2-Ibid., p. 119.

circumstances, other fluids of the same animal flow also to the same places, and especially nourishing fluids, it must follow that two or more tentacles will appear and develop insensibly on the points referred to."[1]

Lamarck gives as another example the origin of hoofs in mammals:

"All mammals sprang from saurians, more or less similar to our crocodiles. They first appeared under the form of amphibian mammals with four feebly developed limbs. These primitive forms divided in the manner according to which they fed. Some, accustoming themselves to browse upon shrubs, became the source of ungulates. Advancing upon the earth, they experienced the need of having longer limbs, their toes became enlongated, and the habit of resting upon their four feet during the greater part of the day has caused a thick horn to arise, which envelops the extremity of the toes of their feet. The other mammals remained amphibious, like the seals."[2]

He also explains the origin of horns in ruminants by the efforts which they have made to butt their heads together in their period of anger, thus forming a secretion of matter upon the head.[3] These illustrations are very crude and highly incredible.

His account of the limbs of snakes is till cruder and somewhat amusing:

1-Osborn, H. F., From the Greeks to Darwin, p. 169.
2-Ibid., p. 169-170
3-Lamarck, op. cit., p. 122.

"Snakes, however, have adopted the habit of crawling on the ground and hiding in the grass; so that their body, as a result of continually repeated efforts at elongation for the purpose of passing through narrow spaces, has acquired a considerable length, quite out of proportion to its size. Now, legs would have been quite useless to these animals and conseqently unused...The disuse of these parts thus became permanent in the various races of these animals, and resulted in the complete disappearance of these same parts,..."[1]

Lamarck's speculations far outran his observations and the absurd illustrations he used placed his really sound speculations in a position to be ridiculed by his critics. The stigma placed upon his writings by Cuvier, who greeted every edition of his work as a "nouvelle folie" and the disdainful allusions to him made by Charles Darwin placed him in the light of a purely extravagant speculative thinker.

Charles Darwin (1809-82) and his theory of Natural Selection did much to displace Lamarck's idea of the transmission of acquired characters from the position of importance which it held with the revival of evolution. Darwin spoke of Lamarck in a manner which he never used to describe any other naturalist.

"At last," he writes, "gleams of light have come, and I am almost convinced (quite contrary to the opinion I started with) that species are not (it is like confessing a murder) immutable. Heaven forfend me from Lamarck's nonsense of a 'tendency to

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1-Lamarck, op. cit., pp. 18-19.

progression,' 'adaptations from the slow willing of animals,' etc. But the conclusions I am led to are not widely different from his; though the means of change are wholly so." In another place he wrote: "Lamarck's work appeared to me to be extremely poor; I got not a fact or idea from it."[1]

While Darwin disdained pure Lamarckism, yet he was forced into the belief, from his observations, that acquired modifications were inherited and that organs developed with use or atrophied with disuse and were thus passed on. His mechanism for the transmission of these traits was natural selection. "The preservation of favourable individual differences and variations," he writes, "and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest. Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions..."[2]

"We have good reason to believe, as shown in the first chapter, that changes in the condition of life give a tendency to increased variability; and in the foregoing cases the conditions have changed, and this would manifestly be favourable to natural selection, by affording a better chance of the occurrence of profitable variations. Unless such occur, natural selection can do nothing. Under the term of 'variations,' it must never be forgotten that mere individual differences are included. As

1- Osborn, op. cit., pp. 235-236.
2Charles Darwin, Origin of the Species, 1931, pp. 98

man can produce a great result with his domestic animals and plants by adding up in any given direction individual differences, so could natural selection, but far more easily from having incomparably longer time for action."[1]

"How fleeting are the wishes and efforts of man! how short his time! and consequently how poor will be his results, compared with those accumulated by Nature during whole geological periods! Can we wonder, then, that Nature's productions should be far 'truer' in character than man's productions; that they should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship?"

"In looking at many small points of difference between species, which, as far as our ignorance permits us to judge, seem quite unimportant, we must not forget that climate, food, &c., have no doubt produced some direct effect. It is also necessary to bear in mind that, owing to the law of correlation, when one part varies, and the variations are accumulated through natural selection, other modifications, often of the most unexpected nature, will ensue."[2]

"...A structure used only once in an animal's life, if of high importance to it, might be modified to any extent by natural selection; for instance, the great jaws possessed by certain insects, used exclusively for opening the cocoon - or the hard tip to the beak of unhatched birds, used for breaking

1 Darwin, C., op. cit., pp. 100
2-Darwin, C., Origin of the Species, pp. 102-105.

the egg."[1]

Elsewhere, Darwin explains use and disuse. "In some cases we might easily put down to disuse modifications of structure which are, wholly, or mainly, due to natural selection." The wingless condition of so many Madiera beetles, according to Darwin, "is mainly due to the action of natural selection, combined probably with disuse. For during many successive generations each individual beetle which flew least, either from its wings having been ever so little less perfectly developed or from indolent habit, will have had the best chance of surviving from not being blown out to sea; and, on the other hand, those beetles which most readily took to flight would oftenest have been blown out to sea, and thus destroyed."[2] He explains the blindness of cave animals as another example of the effects of disuse. "As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, their loss may be attributed to disuse."[3]

Thus the theory of the transmission of acquired characters continued to reign under the aegis of evolution and with the modification of natural selection until the time of August Weismann (1834-1914), "the first really original evolutionist after Darwin." He realized that progress in explaining the causal basis of evolution lay in a further investigation of the causes of variation and the physical basis of heredity.

1-Darwin, op. cit., p. 106.
2-Ibid., p. ~~168~~ 169
3-Ibid., p. 171.

The result was the Weismannian theory of germinal continuity which, it seems, has dealt a lethal blow to the theory of the inheritance of somatic modifications. According to this view the germ plasm is immortal and is perpetuated from generation to generation by the mechanics of maturation, each germ cell being the product of the division of a previous germ cell back to the first germ that arose at the dawn of life. Thus the germ cannot be the product of the soma, but the soma is the product of the germ cells.

"As far as I can see," Weismann writes, "there are only two ways in which such a variation could conceivably occur in the germ-plasm in consequence of a corresponding somatic variation. We should either have to assume the presence in all parts of the body of definite tracks along which each somatogenic variation might be transferred to the germ-cells, in the germ-plasm of which it would produce a corresponding change; or else that gemmules, such as Darwin supposed to exist, are given off from every somatic cell and are conveyed to the germ-cells, - either through the vascular system, when one exists, - or by some other means, and that they must then penetrate into these cells, and become incorporated in their germ-plasm. Thus either the presence of hypothetical tracks along which a modifying, though totally inconceivable, influence might be transferred to the germ-cells, or else the discharge of material particles from the modified organ, must take part in the formation of the germ-plasm; there is no

third way out of the difficulty."[1]

"...It would probably be useless even to expect an answer to the question as to how a part, such as a muscle, enlarged by functional hypertrophy, is capable of producing a specific nervous current signifying 'enlargement.' If such an explanation were attempted, we should be compelled to imagine that every cell in the body was placed in communication with every germ-cell of the ovary or spermarium by means of a large number of nerve-tracks, and was capable of continually sending information to the germ-cells of what was occurring in its own substance, and of the manner in which it was influenced, and also of giving instructions how each of the millions of units in the germ-plasm should behave. I believe that it would be impossible to avoid absurdities in explanations of this kind, and consider the whole idea inadmissible."[2]

"It is impossible to assume the transmission of somatogenic variations in any theory which accepts the nuclear substance of the germ-cells as germ-plasm or 'hereditary substance'; for it is theoretically impossible to account for these variations, no matter how ingeniously the theory is constructed."

"At the present day I can therefore state my conviction still more decidedly than formerly, that <u>all permanent - i.e., hereditary - variations of the body proceed from primary modifications of the primary constituents of the germ</u>; and that neither injuries, functional hypertrophy and atrophy, structur-

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1-Weismann, A., The Germ-Plasm, p. 393.
2-Ibid., p. 393-394

al variations due to the effect of temperature or nutrition, nor any other influence of environment on the body, can be communicated to the germ cells, and so become transmissible.

"This statement naturally implies the rejection of Lamarck's principle of variation; for those factors which this talented philosopher and investigator believed to be all-important in the modification of species, - viz., the use and disuse of parts - can have no direct share in the process..."

"The fact, however, that we deny the transmission of the effects of use and disuse, does not imply that these factors are of no importance; and I have already attempted to show in former essays that both use and disuse may lead indirectly to variations, - the former wherever an increase as regards the character concerned is useful, and the latter in all cases in which an organ is of no longer of any importance in the preservation of the species, and in which, so far as the disused organ is concerned, 'panmixia' occurs."[1]

Consequently two schools of thought have arisen with the Weismannian in an undoubted ascendancy, and each school claims to see in embryology and paleontology proof that the causes of evolution are within their explanations. Darwin saw in the thickened epidermis on the soles of the feet of the human embryo the inheritance of an acquired character. "In infants long before birth," says Darwin, "the skin on the sole of the feet is thicker than any other part of the body; and it can

1-Weismann, op. cit., pp. 395-396.

hardly be doubted that this is due to the inherited effects of pressure during a long series of generations." The African Wart-hog (Phacocherus) offers to some naturalists some evidence of the inheritance of somatic modifications. It has a peculiar habit of kneeling down on its fore-limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind limbs. It has a strong horny callosity protecting the surfaces on which it kneels, and these are seen even in the embryo. Selectionists see in this "simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection."[1]

Weismannians offer their own explanation of these callosities. They point out that the mud-puppy (Necturus maculatus) has a much thickened sole, yet it is very primitive living as it does under water, and never exerting great pressure on its soles. "Nor . . . is it <u>reasonable</u> to suppose that it ever had any ancestor who did so for the hands and feet of the Amphibia are the most primitive and ancient hands and feet to be found in the animal kingdom without any known ancestral types. The thickening of the skin on the sole of the mud-puppie's feet <u>must</u> be due, <u>therefore</u>, to germinal determiners and in no way an acquisition through use."[2]

Duerden (1920) "shows that the sternal, pubic, alar and median mesotarsal callosities are already well defined in the unhatched ostrich. Now curiously enough the first three

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1-Detlefsen, J. A., The Inheritance of Acquired Characters, Physiol. Rev., Vol. 5, p. 247-248
2-Ibid., p. 248.

callosities occur exactly in those regions where they would develop through the daily habits of the ostrich. Duerden also suggests that the last callosity (mesotarsal), although unused at present, may be related to the ancestral three-toed condition, in which condition the ostrich would have rested squarely upon its ankle. With the loss of the inner or second toe the whole tarsus would tend to turn inwardly and the median callosity would become unnecessary but has persisted up to the present time. Duerden shows that a new lateral-mesotarsal pad is not represented in the embryo, but develops when the chicks are a month or two old; for instead of resting its weight when in a crouching position squarely on the hereditary mesotarsal callosity, it supports itself on the inside of the ankle, thus giving rise to an adaptive somatic character."[1]

There is perhaps no phase of biology in which writers are so prone to commit logical fallacies as in this field and over and over again interesting examples of begging the question or reasoning in a circle appear in both the Lamarckian and Weismannian camps. Both groups resort to well-known methods of argument in which cleverly worded premises are taken for granted.

"Other similar cases lead to the same sort of dilemma from which there is at present no completely satisfactory escape. Whether we speak of the blind fish or amphibians of dark caves, or of the asymmetrical loss of pigment in the flounder, . . . or even of pigment-variations in the human race we are usually left in a

1-Detlefsen, op. cit., p. 249.

state of doubt."[1] And the arguments could be carried on ad infinitum and ad nauseam, for all the foregoing discussion has dealt with circumstantial evidence which is frankly indirect. Such evidence does not <u>prove</u> the inheritance of acquired characters, and it must usually admit the possibility of several alternative explanations. Such a situation is highly unsatisfactory and productive of nothing. It is necessary then to proceed along experimental lines.

[1] Detlefsen, op. cit. pp. 251

PART III

EXPERIMENTAL EVIDENCE

KAMMERER

Kammerer (1924) has taken unto himself the role of champion of Lamarckism and has conducted several experiments to prove that acquired modifications are transmissible.

The midwife toad (Alytes obstetricans) does not deposit its eggs in water. This species lays only eighteen to thirty-four eggs, which are comparatively large as they contain a generous amount of yolk. The emerging tadpoles have no feet, but they have inner gills. The development from this point on is analygous to that of other toads and frogs; first they are two-legged creatures, then four-legged; next the tail atrophies; and after this the little toad changes his abode from water to land. Kammerer attempted to accelerate the toad's change from water to land. The development of the egg was speeded by heat and at the same time care was taken to slow down all those movements which tended to facilitate the emerging of the tadpole from the egg by subjecting the egg to more than normal aridity and darkness. Gigantic eggs developed which were burst by the tadpole only when they had already grown their hind legs. These tadpoles developed into dwarf-like toads which thereafter from generation to generation produced eggs that were fewer in number but larger and richer of yolk. If the environment continued to be warm and dry, the tadpole emerged

from the eggs with completely developed hind legs. If restored to normal conditions, tadpoles were produced with just the beginnings of hind legs.

In a second and correlated experiment, Kammerer led the midwife toad to seek the water due to high temperature. Under such a condition the toads mated in the water, whereas normally they mate on land. The eggs remained in the water and a few produced tadpoles with outer gills, and the tadpoles when mature were larger than normally. The "water eggs" of later generations obviously become poorer of yolk and therefore smaller; but the gelatin-like cover becomes thicker and thicker. Tadpoles from water eggs of later generations showed a gain of dark coloring matter, and a progressive loss of yolk until the yolk sac ultimately vanished. The gills became shorter, simpler and coarser, and while usually only the first branchial arches of the skeleton are possessed of gills, in the "great-great-grandson generation" all of the three gill arches had gills.

"Possibly to be better adapted to the more difficult seizing of the female in the water, the male of this, (fourth) and, to a certain extent, the male of a previous generation also develop a rough, blackish nuptial pad . . . , on their fingers and forearm. Besides, the muscles of the arm are strengthened, which in turn results in giving the forelimbs a more converging position. All of these exterior sex characteristics, to be found in all frogs and toads, which mate in the water, but are ordinarily not to be observed on the Midwife Toad, which normally mates on land."

"If one admits the atavistic character of the second group of experiments ('back to water, renouncing the care of eggs'), one absolutely cannot avoid admitting that the first group of experiments (gigantic eggs, prolongation of post-maturity on land) amounts to a genuine new acquisition. In the first instance, the whole embryonal and post-embryonal (larval) development is passed in the water, even including the actual fertilization of the eggs. In the second instance, a development more prolonged than under normal conditions is passed outside the water. The stage of living in the water commences, just as under normal conditions, at the moment when the tadpole emerges from the egg, but the latter leaves the egg in a far more progressed stage of development. From this stage of development it does not take as long as before to change again into a land toad.

"If the development in the one direction - 'back to the water' - constitutes regression, the development in the other direction - 'away from the water' - can mean nothing but progression."[1] Kammerer says this "unassailable proof of genuine inheritance was brought about here by the aforementioned controlling tests and strengthened by the fact that, in crossing 'abnormal' Midwife Toads with 'normal' ones, the hybrids are subject to the Mendelian Rule."[2]

His famous experiments with the black and yellow spotted salamanders scarcely need be mentioned. He placed some on a

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1-Kammerer, The Inheritance of Acquired Characters, pp. 53-55.
2-Ibid pp. 60

black background and some on a yellow background. The black areas increased on those on the dark background, while the yellow spots grew larger and larger on those on yellow backgrounds. And Kammerer claims these modifications were inherited to some degree.

Kammerer has spent many years in "proving" the inheritance of acquired characters. The mere fact that the Viennese biologist is the plumed knight of Lamarckism casts serious doubts *a priori* on the value of his experiments. Then again the fact that all his experiments prove so indisputably that somatic modifications are inherited casts still more doubt on the value of his work. And do his experiments with the midwife toad (Alytes obstetricans) prove anything but the effect of environment upon the development of organisms? The fact that these eggs were larger and richer of yolk when subjected to aridity, and vice versa when subjected to water, merely shows the adaptability of the eggs. If the dwarfs of the first experiment and the giant toads of the second experiment were genuinely modified, why were not these conditions passed on to subsequent generations? Kammerer admitted that these modifications disappeared within two or three generations. The fact that gills and nuptial pads appeared merely illustrates atavism, which Kammerer admits. His experiments with the midwife toad may be ascribed to the response of the toads to a selective environment and hence in no way "unassailable proof of the genuine inheritance" of an acquired character.

His experiments with the spotted salamanders are likewise valueless since his records terminated at just the crucial time when they should have been continued to show the inheritance of these changes. Further this experiment has come under the suspicion of not being honest.

OVARIAN TRANSPLANTATIONS

In an ingenious experiment Castle and Philips (1911) transferred ovaries from two young black guinea pigs to an albino female where ovaries had been removed. The albino was then mated to an albino male and all of the six young were black - exactly the same result would have ensued if the albino male had been mated to a black female.[1]

This experiment stands as good evidence against the transmission of acquired characters. The germ cells were in the new environment for ten months and yet were not in the slightest way modified by the changed environment. However, this experiment has been criticized on the ground that the lack of color cannot be expected to change a color. In other words, we cannot expect albinism, which may be due to lack of enzymes in somatic cells, to modify germ cells.

1-Castle, W. E., Genetics and Eugenics, p. 66.

MUTILATIONS

Colton (1931) amputated the legs of rats to see if this loss would be transmitted in any way. Albino rats were selected from the strain of the Wistar Institute experimental colony because their vital statistics are complete and the dimensions of the bones capable of statistical treatment. From these rats the forelimbs were removed under ether, four to twelve days after birth. They were then raised in special cages that allowed a six-foot run. The biped rats so produced were bred for six generations. In the first generation one half of the litter was not operated on and these constituted the control. In compiling the tables of results, the bones of each operated rat were compared with a control of equal skull length. This was accomplished through the preparations of curves of femur length, etc. By means of these curves, from the femur length of the operated rats, the femur length of the control rat of equal skull length is subtracted. The same process is repeated for tibia length, for tibia breadth and for mesial bend of the fibula. From these differences, means, standards of deviation and standards of errors were computed by ordinary methods.

The results showed what is universally accepted, a sustained use of an organ increases the size of the organ during the period of growth. On this point, the differences between the first generation of operated and control are "overwhelmingly significant." "Taking everything, all in all, it is

important to note that the tibialis posticus and anticus on the lateral side of the fibula increase while the flexor group on the mesial side of fibula decrease."[1]

The results failed to show a progressive change to the fifth generation, thus indicating that acquired characters are not inherited. Colton concludes that "As far as the Lamarckian factor in evolution is concerned the experiments are negative."[2]

Calkins (1911) undertook the difficult task of cutting the cells of paramecium whose power of regeneration is very poor and whose nuclear material is rather highly concentrated. The aim was to ascertain what happens in a cell in which the power of equilibrium is suddenly disturbed. Calkins succeeded in cutting thousands of paramecia successfully. Since the animal died if the nucleus was cut, it was necessary to divide the animal into unequal parts. The part without the nucleus, whether the anterior or the posterior, dies without division in a majority of the cases. In a few cases when division took place in the major portion of paramecium, the division was abortive and a monster resulted. After such a division into a normal and abnormal cell, the normal cell continues to divide normally and forms a race of individuals unaffected by the operation. The abnormal cell in some cases divides again asymmetrically and forms another normal cell. In other cases the second division is abortive and monsters are formed. In a

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1-Colton, H., A Lamarckian Experiment, Amer. Nat., Vol. 65, p. 349
2-Ibid., p. 350.

few cases it continues to divide with a gradually decreasing abnormality until normal forms are regained. Finally, in many cases they died without further division.

Peebles (1912) undertook a study of the regenerative power of single individuals. Part of the work aimed at producing a smaller race when the cytoplasm was cut. The methods used were practically those of Calkins (1911), except that the cultural media differed. A long series of work was done on pure lines in an attempt to produce a smaller race where the average size was definitely ascertained before the operation was performed. Measurements made on the cells of the first few generations of the truncated progenitor would lead to the conclusion that it is not only possible but a simple matter to produce a small race from a large one. The first few generations produced a normal sized individual and a smaller individual. This production of a small and a normal individual continued for four generations; in the fifth generation both offspring were fully as normal and exactly the same size as the control race.

The work of Colton (1931), Calkins (1911), and Peebles (1912) can be legitimately objected to on the ground that mutilations are not the acquiring of a character but the dropping off of a character. Hence, these mutilations cannot stand as evidence against the transmission of acquired characters. However, Colton points out that the removal of the forelimbs led to a marked increase in the size of the tibialis posticus and the tibialis anticus, and a decrease in the flexors of the leg.

Breeding these biped rats for six generations failed to show any inheritance of the modified condition of the muscles. This part of Colton's work stands as evidence against Lamarckism.

TEMPERATURE

To test the hereditary adaptation of Drosophila to higher temperature, Northrop (1920) placed cultures of imagos which had developed at 20° and 32°C in incubators at 29°, 32°, and 33°C. The aevelopment was as follows: those imagos which developed at 20°C and were place at 29° or 32°C were able to produce eggs capable of developing at those temperatures. Eggs producea at 33°C did not develop beyond the pupal stage. Imagos developed at 32°C were unable to produce eggs capable of developing at a higher temperature than 32°C. It was not possible to raise more than one generation at 29°C or over unless the culture was removed to a lower temperature for at least twenty-four hours every generation. A culture was continued at 30°C by this method of intermittent cooling for over ten generations without any noticeable change in the upper temperature limit. A second culture has been kept continuously at 28°C for fifteen generations, and in this case there was no change. The organisms were still unable to grow for more than one generation at a continuous temperature of 29°C or over.

Krafka (1920), working on the effects of temperature upon the number of facets in the bar-eyed mutant of Drosophila, reports that "Neither inheritance nor induction effects are exhibited by this material."[1]

The size of the eye of Drosophila is dependent on several known hereditary and environmental factors. An environmental

1- Krafka, The Effect of Temperature, Jour. Gen. Physiol., Vol. 2, p. 463.

factor may just balance a hereditary one so that the results are indistinguishable. Zelany (1928) found that when bar-eyed stock were raised at 27°C, it resembled individuals raised at 17°C which have changed in hereditary constitution from bar to ultra-bar. That is, the somatic effect of a change in hereditary constitution from bar to ultra-bar eyes has a temperature equivalent of approximately 10°C.

This material seemed to furnish ideal conditions for the study of a possible transfer of somatic temperature effects to the offspring. While a general observation of bar-eye stock over a period of ten years failed to show a marked inheritance of temperature effect, it was felt desirable to test the possibility that there may be a slight effect in each generation which is cumulative and noticeable after some generations have elapsed.

The experiment was started with an inbred selected stock of a known history, and if a single pair was kept at 17°C, the others of the stock were kept at 27°C. At the lower temperature, the size of the eye and the corresponding number of eye facets is about two and a half times as great as at the higher temperature. Tests for changes in inherited constitution were made at intervals by reciprocal transfers of some of the individuals from one temperature to the other. At each test there was a comparison of flies raised continuously at one temperature with flies raised at that temperature for one generation whose ancestors had been kept for many generations

at the higher (or lower) temperature.

After the flies had been raised at the two separate temperatures for five months, the 27° line was in the eleventh generation and the 17° line in the fifth generation. Twenty single pair matings of the 27° line were put at 17° in the same incubator with the continuous 17° line. Correspondingly, twenty single pair matings of the 17° line were put at 27° in the same incubator with the continuous 27° line. Two reciprocal comparisons may therefore be made. One the one hand, the flies whose history is five continuous generations at 17° were compared with those whose history is eleven generations at 27°, followed by one generation at 17°. On the other hand, flies whose history is eleven continuous generations at 27° were compared with flies whose history is five generations at 17°, followed by one at 27°.

Similar tests were made after three months. The results failed to show any significant inheritance of the temperature effect during the recorded period. The experiment is being continued.

These three investigators have failed to find any transmission of temperature effects in their work with Drosophila. The first culture of Northrop's (1920) which was kept at 29° C or over with intermittent coolings for ten generations cannot be used as evidence against Lamarckism since this culture did not become adapted to the high temperature. Therefore, this culture cannot be expected to pass on what it has not acquired.

But the failure of the second culture to become adapted to 29°C and over, after having been grown for ten generations at 28°C, is evidence against the transmission of somatic modifications. The failure of Zelany (1928) and of Krafka (1920) to find any inheritance of an increase in the size of the eye and of the number of facets may also be stated as evidence against Lamarckism. Zelany carried one line for eleven generations and another for five generations, and both lines showed no inheritance of somatic modifications.

Realizing that often when testing for the transmission of acquired characters the germ plasm is altered, not the somatic tissue, Sumner (1915) has taken care to attack this problem by means of producing a purely somatic modification. He experimented with heat on the white mouse, thus ensuring a somatic modification. He used two rooms; one, the cold room, was situated on the upper floor of an unheated building and freely ventilated by two open windows. The warm room was heated by a large steam radiator. Obviously the temperature conditions could be maintained only during the colder months of the year, November to April. The average temperature for the warm room was 76°F and for the cold room 38°F.

Then at a certain time in the experiment (April) the temperature differences were discontinued entirely. Thereafter all of the mice were kept in a common room where the temperature in the summer approximated that of the warm room and care was taken that the temperature was identical for both the

offspring of the warm and cold room parents. The measurements were weight, body length, tail length, foot length, ear length, and weight of hair after removal from skin. Since these differences were slight, a special dial caliper was constructed for measuring. "Each measurement was taken twice, and the dial or scale of the instrument was so held ~~so~~ as to face away from me, in order that the reading might not be known until the measurement was completed."[1]

Some 1300 mice were subjected to these conditions, but unfortunately the author found it impossible to carry the experiment beyond the first filial generation due to the high pre- and post-natal mortality. This experiment was repeated on four different groups of rats on four different occasions. But from none was it found practicable to secure a F_2 generation.

Throughout the experiments, differences between the mean measurements of lots which were reared in the cold room and ones which were reared in the warm room were compared. As regards two parts, the tail and the foot, these differences were considerable in amount, and of "absolutely certain statistical significance." In all four experiments, they were always in favor of the warm room animals.

In the warm room series, tail length was considerably greater than in the cold room series. The foot length was likewise "unmistakably modified in the same direction." With ear length the result was inconsistent and uncertain. Lastly

1-Sumner, F. B., Some Studies of Environmental Influence, Jour. Exp. Zool., Vol. 18, p. 339.

the hair length was found to be considerably greater for the cold room series. Weight was not appreciably affected in either series.

In the offspring of these modified parents born and reared in a common room, those of warm room parentage had on the average a greater weight and greater length of tail, foot and ear than those of cold room parentage, the conclusion being based on four different lots, these differences being such as have been used to distinguish northern from southern mammals.

Circumventing the criticism that these differences were due to temperature effects on the female during pregnancy, Sumner points out that in no case did mating take place during the experimental periods. And he concludes:

"At no time have I ever declared my results to be proof of, or even evidence for, the 'inheritance of acquired characters.' Indeed, I have ~~often~~ insisted that in the present state of our problems this latter expression has become hopelessly obsolete. As regards the various possible interpretations of my results, I have always expressed indecision."[1]

This experiment loses whatever significance it may have had because Sumner carried his experiments no farther than the F_1 generation. While the F_1 did show an inheritance of temperature effects, this experiment cannot be used to support the contention of the Lamarckians.

1-Sumner, op. cit., p. 328.

A series of experiments in which Leptinatarsa decim-lineata was introduced into the environmental complexes of the deserts at Tucson, Arizona, in nine years of experimentation have shown how the introduction of an organism from one habitat to another, here from a mesophytic to a desert environment, produces alterations of the water relation in ways that "are adaptive and inheritable in character."

The specific result of the experiment concerns the development of the organism, during the periods of the experiments, and of its capacity to hold water within the tissues so that the intense desiccation of the dry seasons, which are passed in hibernation, does not result in the death of and elimination of the introduced population. The change is adaptive, right in line with the environmental pressure that is incident upon the population, and in tests is shown to be "gametic." This adaptation, crossing with the normal, behaves as a Mendelian dominant, and is not easily reversible.

Tower (1917) took his material from the laboratories at Chicago, the history, reactions, and genetic composition of the material having been known for generations. Two strains of beetles were used which were raised near Chicago and which were therefore adjusted to the conditions of the place of their origin.

These beetles have two generations a year. They pass the winter in an adult condition, hibernating in the soil, and emerge in the spring, producing the first generation that

matures in July. This F_1 then produces a second generation maturing in late August and September. The F_2 does not breed but undergoes changes preparatory to hibernation in which condition they remain until the next spring. In the changes that take place the waste products are eliminated, the water content reduced, thus lowering the freezing point and preventing death of the insects in the cold winter months. Upon emerging, the water reduction is rapidly compensated for by water derived from the food, and by the absorption of water from the atmosphere by the tissues.

The experiment was conducted at the Desert Laboratory of the Carnegie Institute of Washington. All experiments were conducted in cages thus making complete control possible and thereby protecting the material from predacious animals or other conditions that might have eliminated them.

The beetles showed one interesting response to the desert environment. They developed a capacity to retain water in the tissues of the hibernating generation rather than of reducing it, as is the habit.

The development of this modification was first discovered when four hundred individuals representing the F_6 of a line were sent to Chicago early in September and placed in cages where they soon hibernated. However, they absolutely failed to survive the Chicago winter and were completely eliminated, while a culture of the parent stock in a cage six feet away showed only the normal reaction to that particular winter.

A further test was made, the F_7 generation being crossed with the normal Chicago strain. The result was a completely eliminated F_1, showing a complete dominance of the condition present in the Tucson parent. The Chicago stock, to the contrary, although raised in exactly the same environment, showed the usual rate of survival.

Continuing the experiment, Tower crossed a Tucson F_{10} with a Chicago stock. All the F_1 hybrids were eliminated, not one appearing in the spring, again showing the complete dominance of the Tucson trait over the original or normal condition at Chicago. Crossing a Tucson F_4 with a Chicago stock resulted in the survival of three hybrids; crossing a Tucson F_2 resulted in the survival of seven hybrids. In the F_2 hybrids in both cases, out of 2,137 that hibernated, 443 emerged. Random matings were then made from these of twenty females and twenty males. The F_3 showed no variation from the Chicago stock. The experiments have been conducted for nine years, the results of which show that the condition of non-capacity to survive the winter at Chicago is a gradually increasing product of the populations at Tucson and that the behavior in crossing the Tucson characters is uniformly one of a Mendelian dominant, the normal Chicago condition appearing in numbers as close to what could be expected.

Undoubtedly a modification has taken place as a result of the change from a moist habitat to one of intense desiccation. Tests show that the Tucson materials, especially after the

sixth generation at Tucson, have constantly the capacity to hold the water content, are more resistant to desiccation, and in every way differ in reactions to the water loss from the same materials that have lived at Chicago constantly. The elimination of the Tucson stock at Chicago is clearly due to its inability to release the water in the tissues with sufficient rapidity to keep the freezing point below the temperature of the soil. Consequently they are frozen to death by the decreasing temperature accompanying the onset of the northern winter. Examinations show that few of the individuals in the test survive beyond December first and none at the end of the month. Further, many of the individuals recovered for examination had frost crystals within the tissues and extensive disruptive actions therefrom.

"What the alteration has actually been in the mechanism of the organism, I do not know," confesses Tower. "Thus far I have not been able to detect any anatomical modifications, or changes of a cytological character that have taken place. Water loss in these animals is through the dermal glandular secretions and respiratory activity. As far as I can determine, there is no decrease in the dermal glands,....although I have searched diligently therefor. Moreover, there are no indications of a thicker cell wall, either in the hypodermis or ~~in the~~ of any increased thickness in the cuticular linings of the tracheal tubes.

"Whether it is due to changes in the permeability of the

cell membranes or to changes in the colloidal contents of the cells is a matter of opinion, as I have no evidence that supports either view with any certainty, and accurate determination of either of these is difficult, if not quite impossible. Regardless of what the actual change may consist of, it is an evolutionary modification, that is directly adaptive in response to altered conditions of life, and as such is well worth careful examination and further investigation."[1]

Lest readers jump to the conclusion that results of this kind are easily obtainable, the author introduced several other species into the same environic conditions at the same time, and the same care and persistency has been used with these species, namely, signaticollis, diversa, undecim-lineata, panamensis, multitaeniata, oblongata, haldemani, juncta, and dilecta. None of these has produced anything like the results described in decim-lineata.

"The most plausible interpretation of the results of these experiments is that we are dealing with a case of the response of the entire introduced population, of a uniform composition and behavior, in a determinate variation in Darwin's sense,"[2] Tower concludes.

Tower's (1917) experiments with the beetle Leptinatarsa decim-lineata appear to have produced alterations in the abilities of the insect to release its water content that are

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1-Tower, W. L., Inheritable Modifications of the Water Relation..., Biol. Bull., Vol. 33, pp. 244-245.
2-Ibid., p. 254.

"adaptive and heritable in character." As will be remembered, these beetles release the water from their tissues with the approach of winter which they spend in hibernation, thus lowering the freezing point and preventing death.

Now when these beetles were reared in Arizona a number of generations, they developed the ability to preserve the water in their tissues and apparently lost the ability to release the water, for when restored to Chicago they all perished. Further, when crossed with Chicago strains, in all instances the hybrids showed the Mendelian ratios with the modified character being dominant. This may be looked upon as the inheritance of a somatic modification, but it lends itself much more easily to a selectionist's explanation, and it is in this light that the author regards it. The only flaw is that the modified beetles failed to re-adapt themselves in every instance when restored to the normal environment. To the argument that future generations would undoubtedly re-adapt themselves, it may be replied that none of these modified beetles lived through the winter and hence could not produce progeny.

NUTRITION

Powers (1912) accidently discovered a case of heterogenesis in the genus Asplanchna, which appeared as a mutation. Sparsely distributed among a mass of humped rotifers belonging to Asplanchna amphora was a mammoth rotifer of a different type. It was campanulate in form and humpless, with an enormous ciliated corona and a transverse diameter that frequently equalled its whole length. Careful investigation almost convinced Powers that he had discovered a bona fide mutation.

However, Powers found that the humped and campanulate types reproduced each other. But the campanulate never appeared in young stocks and rarely when feeding on normal food. On the other hand, they were invariably present and quite numerous in old stocks. In fact, Powers observed that they appeared only in extremely crowded mass cultures. And while the campanulates rapidly multiplied, the humped type rapidly disappeared. The latter were eaten up by the former, even adults falling prey to the prodigious ingesting power of the campanulates. And in about three weeks the campanulates had practically displaced the humped type.

"It is just possible that these saltational phenomena may be purely local, or at least greatly exaggerated in the genus Asplanchna. The food reactions of this genus are undoubtedly extreme, and the development of their parthenogenetic ova in close proximity to this spasmodic and very variable nutritive supply may possibly make this genus exceptional. But no

fundamental organic phenomenon is wholly isolated and unlike the phenomena of other species. If nutrition can modify the germ cells in the genus <u>Asplanchna</u> and thus bring into existence new types, nutrition surely must be a factor on a wider scale."1

While Power's (1912) work on the polymorphic forms of the rotifer genus Asplanchna seems somewhat afield, the point is that these polymorphic forms arose as a result of environmental conditions. The evidence indicates that the large and strikingly different campanulate form arose only in mass cultures, never in great numbers, and rarely when feeding upon normal food. Moreover, the cannibalistic habit of these giant rotifers appeared to have a definite relation to its sudden appearance. As the author indicates, nutrition in this case appeared to modify the germ cells and hence produce strikingly new types. This, however, is not evidence for the inheritance of a somatic modification.

1-Powers, J. H., A Case of Polymorphism.

CHEMICALS

In certain species of rotifers there is considerable variation in shape and form of the body of the female during the year. Whitney (1916) was of the opinion that Brachionus amphiceros was a variation of Brachionus pala and that it probably could be artificially produced from Brachionus pala at any time by changes in the diets. In rotifers there is some skeletogenous tissue and in most species the greater part of it forms the external covering. In some species the external skeleton is excessively delicate and flexible, while in other species it is relatively thick and non-flexible. This external covering is usually considered as being composed of chitinous material. In general the different forms of rotifers are distinguished from each other by different forms of this external covering. If one could furnish an abundance of material such as the animals use in making the covering, it would seem that there might be an opportunity for obtaining variations in the form and size of the covering. Not knowing how to obtain chitin in a liquid form, other materials were considered. Sodium silicate was used first, and was found to be at once successful beyond all expectations.

Brachionus pala possesses two small anterior spines, one on each side of the base of the tail, whereas the variation, Brachionus amphiceros, not only possesses these two spines which are usually larger, but also possesses in addition two large lateral posterior spines. During the spring and summer

both forms are found, but there is considerable irregularity in their appearance. In the spring Brachionus pala may be found almost exclusively, while later Brachionus pala and Brachionus amphiceros may occur in equal numbers, and still later, from June to October, Brachionus amphiceros may form as high as 93 per cent of the total collections of the two forms. The exact cause of the fluctuating appearance of these two forms in the same body of water is not known.

In the first series of experiments one, two, three, four, and five drops of sodium silicate were added respectively to five jars, each containing 150 c.c. of beef bouillon culture medium. These jars were inoculated with pure cultures of the green flagellate, chlamydomonas. As soon as a vigorous growth of chlamydomonas was obtained, several dozen females of Brachionus pala were put in each jar. After a few days had elapsed, observations were made on the rotifers in these jars which at this time contained many thousands. In the control jars, free from sodium silicate, only three females from nearly 6,000 which possessed the posterior lateral spine were found, while in the jars containing sodium silicate, many of the females possessed the lateral spines. In some of the jars containing five drops of sodium silicate, every female had these additional spines, and so also those in the jars containing ten drops. Not only did the females carry the large additional posterior lateral spines, but their other two posterior spines, as well as their anterior spines, were considerably larger in size than those of the controls.

When the females of Brachionus amphiceros with the lateral spines were transferred to jars of culture media free from sodium silicate, the descendants of these females did not develop the lateral spines but developed into the Brachionus pala type. A few experiments were performed in an attempt to determine whether the rotifers took the silicate out of the water solution or whether the flagellates took it up and the rotifers eating them, obtained the silicate. Chlamydomonas were reared in 150 c.c. culture media containing five to seven drops of sodium silicate. When they had become very numerous and supposedly had taken up as much of the sodium silicate as was possible, they were removed from the siliceous medium and put into fresh media free from sodium silicate. Several dozen rotifers were added. Eight days later two thousand females were observed, but only one had the lateral spines. As yet it is not known that the skeleton contains any siliceous material, but it is considered to be of entirely chitinous material. If this is true, the effect of sodium silicate upon rotifers in causing an increase of the number and size of the spines is certainly not clear.

The fertilized eggs that were produced by the spined females of the Brachionus amphiceros containing sodium silicate produced females of the Brachionus pala type entirely lacking the lateral posterior spines of their mothers. Two hundred and seventy-eight fertilized eggs from such mothers were allowed to develop and none of the females that they produced

possessed the additional spines.

Finesinger (1926) undertook to test the direct effects of various chemical and physical agents on egg production of the parthenogenetic rotifer Lecane inermis (Byrce) and to determine whether any of the effects produced were heritable. Fecundity or length of life can be decreased or cut off by unfavorable conditions, but there is a limit in the other direction. And can the germ cells be so altered that a change in these characters is inherited after the removal of the conditions that originally produced these changes? To test these, certain chemicals ($FeSO_4$, $FeCl_3$, and $NaSiO_2$), alcohol, and diverse temperatures were used.

In all the experiments it was found impossible to get a significant increase in egg production over the normal with any of the chemicals mixed with malted milk fluid. But the addition of $FeSO_4$ and HCl to spring water used as the culture fluid where the organism was without food resulted in a significant increase in egg production over the spring water controls. Alcohol in concentrations of one per cent, 0.25 percent, and 0.50 per cent, when mixed with spring water and kept over distilled water, gave an increase in average egg production and length of life over the controls. The inorganic salts and alcohol exerted a specific stimulating effect upon the organism.

But when the rotifers were kept in spring water over the same percentage of alcohol, there was a marked decrease in egg production in proportion to the percentage of alcohol used.

Clearly these differences of egg production were due to the differences in concentration of the alcohol. When the organism is kept in varied alcohol percentages over distilled water, evaporation of the alcohol takes place and the solution left has a minute concentration of alcohol which acts as a stimulant. When the organism is kept over the alcohol, there is built up a sufficient alcohol pressure to have a depressing effect upon the activities of the organism.

In all the duration experiments, the subjection of Lecane inermis to varied chemical environments and to higher temperatures for a period of three months (about 25 generations) proved ineffective in transmitting diversities beyond the second generation. In some cases complete recovery took place in the very first generation after removal from the chemical environment. In all other cases, there was a definitely marked approach toward the normal during the first and second generations after transfer to normal environment, and a complete recovery in the third.

Whitney's (1916) work is valueless, for he grew only one generation of the females in sodium silicate. Although of the nearly three hundred offspring of the rotifers that had developed additional spines, none possessed these spines, it is not reasonable to expect the modifications of only one generation to become heritable.

Finesinger (1926), on the other hand, carried his lines for twenty-five generations and found no diversities that were

transmitted beyond the second generation. This experiment is evidence against the inheritance of somatic changes.

ALCOHOL

In an extensive work on experimental modification of the germ cells, Pearl (1917) found that alcohol had no detrimental effect on the progeny of fowls treated with alcohol or ether. In Part III he gives the following results.

In the first place, the prenatal mortality was lower for the offspring of treated parents than for the controls. Secondly, the post-natal mortality of all ages was materially lower in the case of offspring of treated parents. Nor was the sex ratio appreciably affected. There was no material difference in the mean hatching weight of the offspring of treated males and the offspring of control males when mated to normal females.

Both male and female offspring of matings in which both parents were treated showed a higher mean hatching weight than the offspring of either completely normal control matings, or of matings in which the father only was treated.

The offspring of the alcoholized parents, whatever the nature of the mating, showed a higher mean adult body weight than the offspring of untreated parents of the same breeds mated in the same way. In the case of male chickens, the offspring of the treated grew faster after the age of a hundred days than those of the control. The same was true of females. In all ages the male chicks and most of the females of those having both parents alcoholic had a mean body weight that was higher than that of those having one parent alcoholic. The

proportion of abnormal chicks produced from treated parents was no greater than that produced from the controls.

The normal Mendelian inheritance was in no way affected.

There was no evidence that the alcoholization of the fowls, whether male or female, had a deleterious effect on the germ cells. Lastly, there was no evidence that specific germinal changes had been induced by the treatment.

Stockard and Papanicolaou (1918) found that in fourteen points considered, the offspring of alcoholic guinea pigs were below the normal controls in thirteen points and equal to the controls in only one point, quite the reverse of Pearl's findings.

The experiment started with forty animals obtained from a reliable breeder. Eleven were males and twenty-nine were females. They were all under a year old, "strong and vigorous in appearance." Three males and six females after test matings were taken for alcoholic treatment. "The choice was entirely ~~at~~ random, there being no evident marks of superiority or inferiority in any of them as compared with the other animals retained as normal control. One of the three males selected for treatment lived to be more than seven years old, and the others were all healthy, strong animals that lived long and bred vigorously."[1]

The treated males were mated with alcoholic females and

1- Stockard and Papanicolaou, Further Studies, Jour. Exp. Zool., Vol. 26, p. 122.

with normal ones; the same normal females were mated with normal males, the resulting offspring constituting the control. From the beginning of the experiment, the same normal female was often mated to alcoholic males and again to control males. The same was true of normal males. This study covers the conditions of 1,170 guinea pigs born from various alcoholic lines as well as from controls.

These experiments all gave results that expressed themselves in some such general way. Therefore, the authors reached the conclusion that "the germ plasm has been definitely modified and the subnormal condition is transmitted through a number series of generations beyond the animals directly treated."[1]

Whitney (1912), working with the rotifer Hydatina senta, found no inherited effects of alcohol. Hydatina senta can be readily reared in a laboratory. Alcohol can be added directly to the liquid medium in which the animal lives. A large amount of liquid is drawn through the mouth, indirectly by means of a pulsating bladder, into the alimentary canal, and the dialyzable parts pass through its walls into the body cavity and then finally out through the excretory ducts to the exterior of the body. In this way the animal is bathed both on the outside and on the inside of the body by the solution in which it is living. Consequently, all internal parts and all organs of the animal are subjected to whatever dialyzable chemical substance may be in the solution. The young females grow to

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1-Stockard and Papanicolaou, op. cit., p. 211.

maturity very rapidly and lay eggs which develop and hatch within a few hours. This extremely short life cycle, from egg to egg in forty-eight hours, more or less, makes this animal a very favorable form with which to work. Many generations can be raised in a short time and as much information gained in weeks as would require years to be gained from some other form.

Four strains descended from the same female were placed in media containing 0.25 per cent, 0.50 per cent, and one per cent alcohol, the fourth strain serving as the control. The results showed that the rate of reproduction was lower for the alcoholic line than for the controls, and further, the more alcohol that was used, the lower the reproductive rate.

Some from the alcoholic lines were removed and put in a $\frac{1}{14,000}$ copper sulphate solution and the power of resistance compared with that of some of the controls put in the same solution. In the controls, ninety-eight per cent lived the whole life-cycle and produced young, while only fifteen per cent of the alcoholics lived and produced young. This shows the susceptibility to copper sulphate is greatly increased by alcohol.

As the one per cent alcoholic line showed the lowest reproductive rate and the least resistance to copper sulphate, this strain alone of the alcoholics was used in testing for the transmission of alcoholic defects, since it was assumed that this strain was injured the most. In the "first water generation" the young females were isolated from the preceding

alcoholic generation soon after hatching and reared in media containing no alcohol. Thus the formation of the egg and all the embryonic development occurred in the alcoholic solution. At maturity this first water generation had a higher reproductive rate than all the alcoholic strains, but did not reach that of the control. This demonstrates that one of the ill effects is partially eliminated in the first generation after the removal from alcohol. In the second water generation the rate of reproduction equalled that of the controls. Thus, in two generations, all effects of the alcohol had been lost.

"These experiments with Hydatina senta are an attempt to determine, in one race of animals only, whether certain alcoholic weaknesses are truly hereditary and the evidence found is negative."1

MacDowell and Vicari (1921) found that alcohol had an effect on the ability of rats of alcoholic grandparents to learn a maze. Experiments were made to test the ability of rats of alcoholized grandparents to learn a maze as compared with controls. In time, distance covered, number of errors, and number of perfect trials, the controls were found to be superior. During the period of learning, the test rats spent more time in running the trials than the controls. In the trials the average of the controls was higher. The test rats covered more distance than the controls, the speed of running showed no sig-

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1-Whitney, D. D., Effects of Alcohol, Amer. Nat., Vol. 46, p. 54.

nificant difference. The test rats made more errors than the controls. More test rats than controls failed to eliminate the simpler errors. The tests made fewer perfect trials and the tests required longer to make a perfect trial.

MacDowell and Vicari conclude: "We believe that the above points show that the test and control rats differ, as groups, in their behavior in the maze. From the standpoint of learning their way to the center and going there for food, the tests are less successful than the controls. The alcoholic treatment of the grandparents is the only basis upon which the rats have been divided into two groups of tests and controls; therefore the alcoholic treatment appears to be responsible for the inferiority of the tests in running the maze. If this is true, a modification of the genetic basis of inheritance is demonstrated."[1]

A comparative study was undertaken by Nice (1912) to test the effects of alcohol, nicotine, and caffeine on the offspring of animals when fed in small amounts so as not to injure their health. Five lines of white mice were carried: one was given alcohol, another nicotine, a third was subjected to fumes of tobacco smoke, a fourth received caffeine, and the fifth was carried for control.

The results showed that the offspring of drugged parents were superior to that of the controls in weight. Tobacco fumes had no appreciable effects. The offspring of alcoholic

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1-MacDowell and Vicari, Alcoholism and the Behavior of Rats, Jour. Exp. Zool., Vol. 33, p. 284.

parents, even when given alcohol, surpassed all the others, and when the offspring of alcoholized parents are not given alcohol, they grow even faster. At eight weeks, while the offspring of the control weighed 16.8 grams, those of the alcoholic parents weighed 19.2 grams, if not alcoholized, and even if alcoholized, they weighed 17.5 grams, still superior to the controls.

Bessie Noyes (1922) selected a hundred rotifers from a mass culture to test the effects of alcohol on the germ plasm. These were reared under normal conditions until each had deposited three or more eggs. Three eggs from each of the hundred were used to start the experiment; one from each individual was placed in a culture dish with one per cent alcohol in the solution used; another with two per cent alcohol; and the third in a dish of tap water.

The cultures were examined daily, the alcohol solutions changed, and the adults transferred to fresh food. This alcohol experiment was carried on for twenty-four weeks in the manner just indicated. A hundred individuals each subjected to 0.25 per cent and 0.50 per cent alcohol solutions,and a hundred controls were allowed to reproduce for a period of two weeks, at which time isolations of a hundred specimens from each line were made, and the egg deposit and length of life for all individuals under each of the three conditions were recorded. Reproduction continued for another two week period, then another isolation was made, etc. until the end of the twenty-third week. At this time the alcohol cultures were discontinued and the progeny from both alcoholic lines were returned

to malted milk solution without alcohol. In this way it was determined whether the effects of the alcohol had any lasting effects on the progeny of the alcoholized progenitors.

At the end of the first week under normal conditions, isolations of the second generation individuals were made for determining the egg production and average life-span. In the line descended from the progeny of the 0.25 per cent alcohol group, the average egg production was 17.77 as compared with 12.33 of the last alcoholized generation. The average life-span differed but little from that of the alcoholic progenitors. In the descendants of the 0.50 per cent alcohol, the average egg production was 13.57 as compared with an average of 3.48 of the last generation of the alcoholic line. The average length of life increased slightly for the non-alcoholic progeny. Those reared continually in the malted milk had an average egg production of 18.56 and an average life-span of 5.56 days.

The individuals of the second generation after the return to normal showed a marked increase in egg production. In other words, there was only a partial retention of the influence of alcohol, and the averages for the generations whose ancestors were subjected to alcohol approached those individuals continually reared in malted milk.

Isolation of the third generation made under the same conditions mentioned showed an average egg production of 21.80 for descendants of the 0.25 per cent alcoholic line and 19.92 for those subjected to 0.50 per cent as compared with an average

of 19.50 for those reared continuously in malted milk. After three generations in malted milk, all the effects of alcohol had been lost.

Hanson and Heys (1927) tested albino rats for the inheritance of eye defects. A litter of ten young from an inbred strain was divided at random into two groups of five each, one group serving as the tests, and the other group as the controls.

The test line was put in air-tight fume tanks placed over evaporating alcohol. This treatment continued daily except Sundays from the age of twenty days to maturity. The rats were left in the alcohol tanks until they were unconscious. For ten successive generations this experiment was carried on. At the end of the tenth generation, the alcoholic treatment was discontinued. Five more generations (eleventh to fifteenth) were raised from both the alcoholic and control lines.

The direct effect of the alcohol on the test line was quite injurious. The eyes became strikingly abnormal, and many rats became blind after a few treatments. The eyes became white or opaque, and sometimes bleeding at the eyes took place during the treatment. Occasionally, the eyeballs collapsed. By the time of maturity, nearly all of the alcoholic rats were blind.

During the period of treatment (ten generations) 1,688 young were born to the alcoholized parents. With the exception of one male, not one of these young exhibited any eye defects. The male with the defective eye was mated to a normal female and sired six litters. Each of these litters were inbred, but

no eye defects appeared. "Apparently in the albino rat it is not possible to transmit by heredity the eye defects induced by direct contact of the eye with alcohol fumes."[1]

In a second experiment, Hanson and Heys (1927) investigated the inheritance of increased resistance to alcohol fumes in the descendants of the tenth alcoholized generation. It was found that the treated rats gradually built up an increased resistance to alcohol fumes. At sixteen days of age, the rats could stand only thirty minutes of treatment with fifty centimeters of alcohol, while at the age of twelve months, they could stand four hours treatment of two hundred centimeters of alcohol.

Thirty descendants of the treated line and thirty descendants of the controls were carried. The individuals of both lines were approximately of the same age and size, hence any differences that may have been due to these factors were eliminated. The animals of both lines were placed in the fume tanks, and the length of time it took for complete narcotization was used as the indicator of the power of resistance. Treatment was given daily for five consecutive days.

The results revealed that no only did the descendants of the treated line show no inheritance of resistance, but they also showed a slight degree of decreased resistance.

Experiments with albino rats on the inheritance of resist-

1-Hanson and Heys, Alcohol and Eye Defects in the Albino Rat, Jour. of Heredity, Vol. 18, p. 347.

ance to alcohol fumes have given negative results.

MacDowell (1927) again investigated the influence of alcohol on the behavior and learning capacity of white rats. He found that the treated rats took longer to run the maze than the controls. The second alcoholized generation was likewise inferior to the controls. The untreated offspring of the first alcoholized generation took a slightly longer time to run the maze than the controls. The second untreated generation, however, showed a marked inferiority to the controls.

All of the evidence presented in this section appears to be self-contradictory. Pearl (1917), Whitney (1912), Nice (1912), and Hanson and Heys (1927) have all failed to find any inheritance of alcoholic defects. On the other hand, Stockard and Papanicolaou (1918), MacDowell and Vicari (1921), and MacDowell (1927) claim that the effects produced by alcohol were inherited. All of these experiments and more seem to be nothing but a mass of futile papers. And the reason for the divergence of results probably lies in the fact that alcohol affects the germ cells. It has a selective action in destroying the weakest germ cells, and it weakens other germ cells. In the case of those investigators who found no inherited effects of alcohol, it may well have been that only the strongest germ cells survived, and hence gave rise to normal or slightly superior individuals. In the case of Stockard, some of the weak cells may have survived and at sexual maturity produced more weak cells. However, the work on alcohol is not a clear-

cut test of Lamarckism, for whatever modifications have taken place are primarily germinal. Hence, these experiments presented throw no light on the problem.

An exception is the experiment of Hanson and Heys (1927), testing for the inheritance of increased resistance. Increased resistance is a somatic modification and, were it inherited, it would be an acquired character in the Lamarckian sense. The experiment, however, shows that acquired resistance is not inherited, and this work that might have lent support to the hypothesis under consideration, produced negative results.

PROTOZOA

"It is often said," writes Jennings (1908), "and it seems to be generally assumed, that unicellular animals differ fundamentally from multicellular ones in heredity. In the Protozoa there is no separation into cells which normally die after a certain period ('somatic' or 'body' cells), and cells which continue to live and multiply ('germ' cells). The parent produces progeny by simply dividing, so that parents and progeny are identical.

"This seems to simplify extremely the problem of heredity, or indeed to remove everything problematical from the subject. Parents and progeny must be alike, it is said, because they are the same. In particular it is commonly held that this removes from the Protozoa all difficulty as to the 'inheritance of acquired characters' - characters added during the lifetime of the individual and due to environmental action, experience, use, accident, or the like. Such characters are in multicellular organisms often called somatic, as distinguished from germinal, and such somatic characters are commonly held not to be inherited. Where there is no such distinction between soma and germ, it would seem clear that there can be no distinction between somatic and germinal characteristics...If the difference really exists, the Protozoa are much more plastic in evolution than are the Metazoa; ....

"'In primitive organisms multiplying by simple fission,

structural modifications acquired during the lifetime of the individual would be carried right on from generation to generation, and hence structural foundations for a whole animal world such as we now see could be laid in a relatively short period as compared with the time necessary to advance organization in forms limited to reproduction by germs. In fact the fundamentals could all be established within the realm of the unicellular Protozoa.'...

"Now, if this difference between unicellular and multicellular organisms actually exists, it is evidently of the highest interest and importance. Yet there have been no investigations of the matter to see if there is really such a difference."[1]

Jennings (1908) undertook to determine whether acquired characters of the Protozoa are transmitted to the offspring.

Jennings takes up first the simplest and most marked characteristics, new appendages, spines, and the like. Next, he considers marked changes in the form of parts of the body, then all things that might be characterized as mutations, abnormalities, monstrosities, and mutilations.

By examining dense cultures of Paramecium, many individuals were found which differed from the usual form or structure. Some had a short, truncate anterior end; others a blunt or truncate posterior end in place of the sharp tip; others were

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1- Jennings, H. S., Heredity, Variation, and Evolution in Protozoa, Jour. Exp. Zool., Vol. 5, pp. 534-545.

crooked or otherwise modified. Many were isolated, and the fate of the peculiarity in question followed. The individuals were placed separately in the concavities of hollow ground glass slides in three or four drops of hay infusion which was changed every day or every two days. The organisms were examined once or twice a day.

Jennings describes in detail a typical case of a new structure, an individual that bore on its body a spine. This case is extremely interesting, because the origin of the peculiarity was observed and its history followed for many generations. The ancestor of the race we are to study was a crooked individual found in a culture where food was getting scarce. It was bent just in front of its middle at a right angle.

The first division showed the crookedness was not to be inherited, though it had its effect on the progeny. The posterior product was normal; the anterior product had two toothe like structures. At the next division, the constriction took place between the tooth-like projections, the posterior individual having the larger projection. Immediately after division, the larger projection grew rapidly larger and longer and sharper as though under pressure, the projecting spine being as long as the body was thick. Thus we have in these two individuals a definite new structure, the origin of which we know, while the organisms were quite normal in other respects. The new structures had arisen during the reproductive process.

We shall follow here only the fate of the large anterior

spine. At the next fission (fourth generation), the spine remained with the anterior product, while the posterior product had no spine. In the fifth generation the spine went to the posterior generation. This spine was followed through twenty-two generations and was found to be transmitted to only one individual in each generation. Thus in the sixth generation there were thirty-two individuals with but one bearing the spine. In the eleventh generation, one out of 1,024 had the spine, and in the twenty-second generation, the spine was found on only one individual out of 2,097,152. This experiment was carried no further, for Jennings found one morning "to his great regret" that the spinated individual of the twenty-second generation had died, due to an unhealthy bacterial condition in the medium. Thus, though the new structure is transmitted, it is not multiplied and there is no tendency to produce a race with this characteristic.

To return to the smaller tooth-like projection on the anterior individual of the third generation, it was found that this small spine persisted through but three generations, being found on only one individual of each generation. In another case the ancestor was short, seeming to lack entirely the posterior half of the body. In the first two fissions, the anterior product was normal, while the posterior product had a blunt irregular posterior end. In the fourth generation there were two normal individuals, one of which bore a short spine. The spine increased in the fifth and sixth generations,

decreased in the seventh, and disappeared altogether.

In the case of individuals with the anterior end truncate, the truncated end persisted for a few generations, being, of course, transferred to but one individual in each generation, and then disappeared. "I followed the history of ten cases of this sort. In all cases the bluntness of the posterior end is transmitted, usually in weakened form, to the posterior individual resulting from division, while the anterior individual is quite normal in form. This continues as a rule for three or four generations, the posterior end approaching after each division more nearly the normal form, till finally regulation is complete, and all the progeny have the usual shape."[1]

In the cases of crookedness or general irregularity of form, the abnormalities were not passed on, but caused modifications in some or all of the progeny for several generations. These modifications were not repetitions of parental forms. In the case of monstrosities where the vital functions cannot be performed, the organism dies.

Lastly mutilations were tried. This was very difficult, but Jennings managed to perform some without killing the organism. A fine glass rod was drawn across an individual near its middle, leaving a deep constriction, while the two halves of the body were swollen. This constriction, however, lasted but a few hours, the organism returning to normal. Likewise blister-like irregularities were produced, but these disappeared in

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1-Jennings, op. cit., p. 608.

twenty-four hours. Many attempts were made to remove part of the endosarc without causing death, but in all cases the animal died. The successful mutilations persisted for two or three generations and disappeared. In one case the mutilation lasted for several generations, but finally resulted in death.

Altogether it is clear that while mutilations may be passed on bodily to certain products of division for a number of generations, there is no tendency for them to be inherited by all the progeny, nor any tendency for all the mutilations to be duplicated in near individuals. A tendency to produce a race of mutilated organisms is no more to be found in Paramecium than in the Metazoa.

The acquired characters thus far described showed no tendency to be inherited; we now come to a case where such a tendency actually showed itself. The difference between this case and the others suggests what must be the nature of an acquired character that is inherited.

There appeared a tendency in one of these spinated lines for adult individuals to remain in chains. In the process of growth the base of the spine became drawn out forming a ridge running along the aboral surface nearly the length of the body. During fission the fission plane did not pass so readily through the ridge as the rest of the individual, so that the two resulting individuals did not separate but remained connected by a bridge passing from the aboral surface of one to that of the other. This union of two individuals after fission reappeared

in successive generations. In the eighteenth and twenty-first generations three individuals formed a chain. In succeeding generations many such chains were formed. In the fifteenth generation Jennings began to save all the progeny of this line, whereas up to this time only the specimens bearing the spine had been kept alive. In the large number of progeny thus obtained, many variants were to be observed in this matter of interconnection. While many individuals were separate, pairs were very common, and chains of from three to eight individuals not uncommon. Fifty generations of such a union were produced in cultures, and at that time unions were still abundant, the number of progeny during fifty generations from the original individuals being estimated at about 1,000,000,000.

Jennings now attempts to answer what the nature of the characteristic must have been in order for it to be inherited.

The characteristic thus inherited was "a modification of the protoplasm of the cell, of such a character as to cause it to behave differently in reproduction."[1] The other characteristics, not inherited, were not such modifications of the protoplasm as to cause it to behave differently in reproduction. In the light of the facts of normal reproduction in the Protozoa and of heredity in general, this difference is an important one. "In order that it may be inherited, a characteristic must be the result of such a modification of the mother cell

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1-Jennings, op. cit., p. 622.

as will cause it to balance in a certain way at reproduction. It makes no difference whether the mother cell in question is a germ cell in a Metazoon or a differentiated Protozoon."[1] A localized inheritance as a spine could become an inherited character "Only through such a modification of the protoplasm of the parent cell as would cause at fission the production of such an appendage on each of the progeny."[2]

Several experiments were carried out on Arcella dentata by Hegner (1919) to determine the effects of environmental factors upon the characteristics of these organisms.

First the effect of underfeeding was noted. Specimens of Arcella dentata were taken from cultures and placed in a medium consisting of one-half distilled water and one-half filtered pond water. A marked retardation of division rate followed. The offspring of the parents showed the effects of the change. They were smaller than their parents in every case. When the offspring were underfed, they likewise gave rise to smaller organisms for the normal of the line, but not smaller than themselves. When, however, these small offspring of underfed parents were returned to normal cultural conditions, their first offspring showed the effects of abundance of food, becoming closer to normal. When full-sized specimens that were produced under normal conditions and which had given rise to small offspring when subjected to underfeeding were again

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1-Jennings, op. cit., p. 622.
2-Ibid., pp. 623-624.

supplied with an abundance of food, the size of their offspring immediately attained normal size for that line.

Then an addition of sodium silicate was tried, for it seemed probable that the presence of an excess of sodium silicate might facilitate shell production and bring about the formation of variations such as longer spines. The method employed was to make up daily, or every other day, culture media as usual and then add one drop of sodium silicate to 100 c.c. of the medium. The results were as follows:

The rate of fission decreased immediately from an average of one division every two and a half days to one every four days. Instead of an increase in spine number and length and in the size of the shell as was expected, the immediate result of the changed medium was a decrease in all these characters. Many of the specimens were badly crinkled; in others the binucleate condition was lost and a uniuncleate condition appeared. In many cases the spines did not extend beyond the edge of the shell, being represented by only ridges on the dorsal surface of the shell.

A third character modified by the presence of sodium silicate was the color of the shell. The shell of an adult Arcella is a very deep brown. The shells of the offspring of parents kept in sodium silicate were a pale yellowish-green, as long as they remained in that medium, but became the normal brown color as soon as they were transferred to normal cultures.

The addition of alcohol was then tried and was found to be

injurious to the organisms.

Then several experiments were made to determine whether temperature affected the length of the spines or not. They were not concluded, but indicated that the length of the spine and of the temperature may be correlated, since the spines of offspring reared at about a temperature of 10°C are smaller than those of their parents which were reared at room temperature.

Hegner concludes that while the environmental factors caused distinct variations in Arcella, yet these modifications persist only so long as the factors are present. "No heritable diversities were observed that were due to the changed conditions."[1]

Woodruff (1917) experimented with Paramecium aurelia to determine the influences of different cultural media on the rhythm of the intracellular reorganization process (endomixis). Four series of experiments were carried on. The cultural media was changed daily in one series, changed every other day in another series, a beef extract was used as the third medium, and Horlick's malted milk as the fourth. These media produced changes in the rhythm of endomixis, but none of these changes was a permanent deviation from the characteristic rate of the species.

De Garis (1927) reports from his experimentally induced monster formation: "My efforts to continue these unusual forms, as such, in pure lines have met with no success. They either

1-Hegner, R. W., Effects of Environmental Factors, Jour. Exp. Zool., Vol. 29, p. 440.

do not survive, or else became regulated to normal types through subsequent division."[1]

Dawson (1926) observed a race of Paramecium that had acquired a modification in some way and which gave promise of being heritable. He found in a laboratory culture of Paramecium aurelia a number of peculiarly truncated individuals. This truncation was so pronounced that the animals were almost exactly two-thirds of the length of the normal Paramecium aurelia. Further studies showed beyond a doubt that these Paramecia had obtained their truncated form by a process of invagination. The first occurrence was in large numbers, it being estimated that at least a thousand such animals were present.

Studies of the mode of formation of the invaginated form have shown animals in all stages of the process of invagination. But it has not been found possible to watch the formation of an invaginated Paramecium which remained in the more permanently invaginated condition. The occurrence of this form has been found, up to the time of writing, only in mass cultures. However, the inciting cause of the invagination process cannot be definitely stated.

Invaginated organisms were isolated and pedigrees of the progeny were made for at least five generations. Five pure lines from invaginated parents were produced, four however were carried for only varying lengths of time. One culture was

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1-De Garis, C. F., A Genetic Study of Paramecium Caudatum, Jour. Exp. Zool., Vol. 49, p. 140

bred for one hundred and ten generations, another for fifty-two, the other two for twelve generations, while the fifth was retained to the present.

Isolations were made daily to see if this modification would persist, since it was found originally in mass cultures. Invariably it has been possible to detect these conditions in isolated cultures. Thus it is seen that under the conditions prevailing in mass cultures as well as in the environment of a daily isolation pedigree culture, the abnormality as originally found was maintained.

The effects of environmental changes were then tried. Commercial spring water, tap water, pureoxia distilled water, and a standard beef-extract medium have been used. "The result with all these environmental changes has been the same, and no change has been observed in the character of the abnormality of form or in its heritability under these diverse conditions."[1]

Dawson concludes: "In the race of Paramecium under discussion. there seemed to have appeared, therefore, the first case of precise inheritance of a modification in a protozoon sufficiently definite to enable the animal possessing it to be recognized with ease as different from the normal type."[2]

"The account given in this paper, therefore, appears to be the first recorded instance in which a new morphological character which is heritable has occurred in a ciliate under

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1-Dawson, J. A., A Mutation in Paramecium aurelia, Jour. Exp. Zool., Vol. 44, p. 146.
2-Ibid pp. 152-3.

culture."[1]

Jennings (1908) and Dawson (1926) have both reported the inheritance of an acquired character, while Hegner (1919), Woodruff (1917), and De Garis (1927) have failed to find any permanent modifications. Neither Jennings nor Dawson, however, produced the modifications that were inherited. In the case of Jennings, the modification was a tendency to remain in chains that persisted for fifty generations, and in the case of Dawson, the modification was an invagination that endured for fifty generations. It seems that these two modifications were something more than somatic; Dawson's case, in particular, seems to be a nuclear modification that found external expression during conjugation. Whether these modifications are somatic or "germinal," it is practically impossible to decide.

There is no doubt, however, that the artificially produced modifications of Hegner, Woodruff, and De Garis are somatic. But neither Hegner nor Woodruff states how many generations were carried, and the monstrosities produced by De Garis either became normal within a few generations or died after the experiment. The time element invalidates the experiments of these three investigators.

1-Dawson, op. cit., pp. ~~153~~, 134.

INCREASED BODY WEIGHT

Donaldson and Meeser (1932) investigated the effect of exercise on the musculature and weight of different organs in the albino rat. Test rats were placed in revolving drum cages in which they took ample exercise for two hundred and twenty-five days. By that time they had produced young. So they were killed and dissected. Seven generations were carried.

As might have been expected, the results showed an increase in the weight of the musculature and of various organs, such as the heart, kidneys, suprarenals, submaxillaries, and gonads. The total body weight of the tests exceeded that of the controls by about six grams. The authors, however, found no cumulative effects of exercise from generation to generation, each successive generation starting with the same normal organ and muscle weight and size.

This experiment is a fair test of Lamarckism. The inctéased size of the muscles and organs is a somatic modification, but at the end of seven generations the data failed to show any evidence of a cumulative effect.

CYTOLYSINS

Since antibodies can be originated in living organisms which will destroy particular tissue elements, Guyer and Smith (1918) ask the question whether or not it is possible to secure a selective action on certain parts of the developing embryo.

In an attempt to answer this and similar questions, the investigators undertook a series of experiments in an attempt to produce antenatal effects in fetuses by means of cytolysins. Rabbit lens was used as antigen and chickens as the source of antibodies. 'The lenses upon immediate removal from the dead animal were thoroughly pulped in a mortar and diluted sufficiently with normal saline solution to permit injection in the peritoneal cavity of the fowl by means of an hypodermic syringe. When the fowl was ready for removal of the serum, killing was found to be more practicable than drawing off the blood. To secure blood in a sterile condition, the fowl was anaesthetized with ether until insensible, the feathers hastily plucked from the neck and later washed in alcohol; the skin was entirely cut around the neck near the head, peeled back, the oesophagus and trachea transected and turned back; the head was then quickly severed near its base with a heavy scissors and the neck thrust into a wide-mouthed sterile test-tube or flask. The blood was then chilled for an hour or more, then centrifuged for twenty minutes to separate the serum from the clot. The

serum, after warming to blood heat, was injected in rabbits in the marginal vein of the ear. All instruments were sterilized.

Five experiments produced some young that had an abnormality of one or both eyes, such as an opacity of the lens, liquefaction of the lens, and dwarfed eyeballs. "The fact of chief interest is that visible specific structural modifications can be engendered in the young _in utero_ by means of specifically sensitized serum,"[1] the authors conclude.

Having come to the conclusion that their results were very significant, Guyer and Smith (1920), in a second series of experiments, took pains to secure completely unrelated stock and thus eliminate the possibility that the eye defects were congenital and not due at all to the lens anti-sera. "To safeguard the experiments in this respect, we have imported rabbits from other States (Minnesota, Iowa, Illinois, and Indiana) and tested them genetically before treating them with serum or crossing them with our original strain."[2]

In reply to the criticism that eye defects are common among rabbits, the authors reply that in all their work with rabbits they have never noticed sporadic eye defects. Several rabbit breeders were consulted, and they all reported that no record of congenital eye defects had been observed by them.

To test whether the eye defects were attributable to the specific action of the antibodies, or merely to a general

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1-Guyer and Smith, Studies on Cytolysins, Jour. Exp. Zool., Vol. 26, p. 82.
2-Guyer and Smith, Studies on Cytolysins, Jour. Exp. Zool., Vol. 31, p. ~~171~~ 172

poisonous effect of the serum, the investigators injected a number of pregnant females with pure fowl serum which had been sensitized to rabbit testis.

The result was that, of the forty-eight young obtained by repeated experiments of this sort, not one was observed to have an eye defect.

The most important result of these experiments was the fact that these eye defects were transmitted to subsequent generations. Up to the time of the writing of this paper, the defects had not only been transmitted to the offspring, but also tended to grow worse with each succeeding generation. The abnormal condition appears, in general, as a Mendelian recessive.

Guyer and Smith conclude: "As matters now stand, we do not feel impelled to insist on either interpretation of the mode of inheritance, still less are we inclined to undertake any categorical exposition of the serological detail. We are more interested in presenting the facts that our experiments have revealed."[1]

Continuing their experiments still further, Guyer and Smith (1924) carried through several generations a new strain of defective eyed rabbits. The results were quite similar to those already obtained, and in general the eye defects behaved like a Mendelian recessive. An attempt was also made to secure eye defects by the injection of pulped rabbit lens directly into

1-Guyer and Smith, op. cit., Vol. 31, p. 214.

the rabbits themselves. One conspicuous success resulted. This offspring, a male, had both eyeballs strongly rotated backward and "chalky-looking lenses." The conditions persisted as an adult and the eyeball began to show signs of collapse. When mater, the defects of this male were transmitted to one of the two offspring that lived, four others having died shortly after birth.

To further establish the investigator' belief that the lens reaction was specific, female rabbits shortly before or during pregnancy were injected with typhoid fever vaccines, living typhoid germs, and with various kinds of foreign serum. Of the five hundred young born after such treatments, not one showed any signs of eye defects.

Disclaiming any idea of advancing their work as proof of Lamarckism, the authors are still more strongly of the opinion "that the germinal constitution can probably be altered by immunological influences,"[1]

Finlay (1924) undertook to repeat the work of Guyer and Smith by injecting anti-lens sera into pregnant mice and rats. Anti-lens sera was prepared in various ways; different species lens was used as antigens. Rat lens, ox lens, and sheep lens were each used as antigens, and the rabbit and the fowl used to provide the serum. The injection of antigen was continued until a definite precipitin reaction could be demonstrated.

1-Guyer and Smith, Further Studies on Inheritance of Eye Defects, Jour. Exp. Zool., Vol. 38, p. 473.

The animals were then bled, the clear serum drawn off, bottled, and used for injection into the pregnant animals as quickly as possible.

The antisera were injected chiefly in female mice, the majority of which were pregnant. The results differed greatly. The anti-rat lens serum was very toxic and mice which received an injection of this gave an average litter of 1.1; the sheep and ox antiserum group averaged 2.9; the control group injected with anti-vitreous humour produced an average of five per litter.

The eyes of the surviving F_1 were all normal. Brother and sister matings were then made in order to allow the greatest opportunity for defective eyes to manifest themselves. But the F_2 generation was also normal. Active immunization was attempted, but the litters were all of average number and were normal in every respect.

In these experiments it is the injection of rat antisera that has the most bearing on the work done by Guyer and Smith with rabbits. "Fortunately they were enabled to rear a number of the affected young which had defective eyes due to the specific influence of the antiserum. But with mice it is difficult to rear defectives, hence it is quite possible that of the many embryos that died, some were effected in a specific manner by the anti-lens serum."[1]

1-Finlay, G. F., Effect of Different Species Lens Antisera, Brit. Jour. Exp. Biol., Vol. 1, pp. 212-213.

In view of the interest which the work of Guyer and Smith stimulated, Huxley and Carr-Saunders (1924) have attempted to repeat the experiments, modeling their methods after those employed by Guyer and Smith.

Lenses used for injection were removed from the rabbits under sterile conditions immediately after the death of the animal. Ox lenses were sometimes used in place of rabbit lens, but the methods employed were precisely the same as in the case of the rabbit lens. The lenses were placed in a mortar and after the addition of a few c.c. of normal saline solution were thoroughly pulped. Since a gelatinous residue remained, no matter how thoroughly the pulping was done, centrifuging was resorted to, which proved to be very satisfactory. But to forestall criticism that the whole of the lens substance had not been injected, centrifuging was later abandoned, and in the later experiments injections were made with as much of the liquid as possible without causing complete clogging of the needle. Guyer and Smith used the intraperitoneal method in most cases and the intravenous in a few cases. Huxley and Carr-Saunders used the intravenous method in a majority of cases, the intraperitoneal in a few cases. Precipitin tests were made from time to time to ascertain whether as a result of this treatment antibodies reacting with lens were present in the blood of the fowls. Every injected fowl showed a positive reaction with the exception of two. Five uninjected fowls were tested and they were all negative.

The serum was then injected in female rabbits. No changes were observed in the eyes of the treated females. A total of fifty-seven offspring was obtained from them. The eyes of all the young were carefully examined in order to detect any abnormality that might exist. All the young rabbits which lived long enough to enable them to be handled were first examined without the aid of any instrument, and afterwards with an ophthalmoscope. The young rabbits proved to be admirable subjects for the use of this instrument. Guyer emphasized the advantages of using albino rabbit owing to the ease of detecting lens abnormalities. But Huxley found that the ophthalmoscope detected any defects in pigmented rabbits as well as in albinos. Some of the young did not live long enough to be tested by the ophthalmoscope. A few were born dead or dying and others died before they could be handled. In such cases the rabbits were examined immediately after death. Careful observation was then made to see if there were any outward abnormalities. The eyes were then removed and the lens dissected out and examined. The results of the examination showed that with the exception of the two cases, "no sign whatsoever of any abnormality affecting the size, shape, or structure of the lens or of any other part of the eye was ever observed by us."[1]

In the first of the two cases, the rabbit was obviously suffering from a marked abnormality of the head region. The

1-Huxley and Carr-Saunders, Absence of Prenatal Effects of Lens Antibodies, Brit. Jour. Biol., Vol. 1, p. 223.

skull was deformed. The upper jaw was twisted to the left; the left side of the face was sunk in and a flap of skin covered the left eye. After it died the skull was macerated. The conclusion reached was that the abnormality centered entirely in the skull. The left eye when dissected out proved to be normal in every respect. "There would therefore seem to be no reason for attributing this particular abnormality to the treatment given to the mother."[1]

In the other case, the lens when dissected out was found to exhibit a pyriform opacity, although normal in size and shape. A series of observations have shown that rabbit lens both from treated and untreated parents, often exhibits opacities a few hours after death. "These opacities, however, so far as we have observed them, were invariably spherical or ring-shaped, while the opacity in the case of the lens from the young rabbit referred to was pyriform. It was also rather more dense than what we may call the normal opacity. Our knowledge, however, of the formation of these opacities under normal conditions is so incomplete that the possible significance of this single observation can not be accurately estimated. It would clearly be straining the facts to assume at the present stage that the opacity in this particular case was certainly due to the treatment to which the mother had been subjected, although it possibly may have been.

"The results of treating the does with sensitised serum

1-Huxley and Carr-Saunders, op. cit., p. 224.

are therefore negative."[1]

The issue of Lamarckism had been a dead one for some years until it was resurrected by the investigations of Guyer and Smith (1918). Their work seemed at last to have shown a way of transmitting a somatic modification. While Guyer and Smith have been exceedingly careful to deny any claim to having proved Lamarckism or any interest in "establishing or disestablishing any ism," yet credit for reestablishing the validity of the Lamarckian principle has been attributed to these authors. Guyer himself has elaborated on the significance of the experiments in such a manner as to imply plainly the discovery of a method for transmitting an acquired character.

However, certain objections have been raised to these experiments. In the first place, the injected parents showed no eye defects whatsoever after the treatment, so there was no transmission of an acquired eye defect from the test parent to the offspring. Further, in all probability, the modifications produced by the lens antisera were germinal and not somatic. Bagg and Little (1924) were able to produce eye defects by means of x-rays, and it is well known that x-rays affect the germ plasm. Hence the work of Guyer and Smith cannot be regarded as the inheritance of an acquired somatic modification.

Moreover, Finlay (1924) and Huxley and Carr-Saunders (1924) have failed to duplicate the results of Guyer and Smith. These

1-Huxley and Carr-Saunders, op. cit., pp. 224-225.

investigators have used the same technique and the same kind of animals with completely negative results. In the light of these experiments and the objections mentioned, the work of Guyer and Smith is unacceptable as evidence for the transmission of acquired characters.

X-RAYS

The work of Guyer and Smith (1918) led Bagg and Little (1924) to investigate hereditary changes in the offspring of mice treated with x-rays. An inbred stock of healthy young mice were divided at random into two groups; one group was irradiated by x-rays, and the other group was kept as a control.

No immediate physiological effects were observed to follow, and the animals remained in good health. While some of the treated animals proved to be sterile, two litters from different pairs of irradiated animals were obtained. These young were normal. But, when inbred, two defective eye males appeared in the F_2 generation. In the fourth generation there were fifteen abnormal-eyed individuals. These abnormal-eyed mice were inbred for ten generations, producing several hundred defective-eyed offspring. In some cases a hundred per cent of the offspring has been defective.

The eye abnormalities were of various kinds. Frequently the eyeball was smaller and the cornea opaque. Sometimes the eyeball was greatly reduced in size and the lens very opaque. Sometimes the optic tract atrophied and the bones of the skull were twisted toward the side containing the defective eye. A marked feature was the close association between defective eyes and club-feet. Of the eighteen club-foot animals, only one did not also have eye defects.

An examination of mice that died soon after birth and of

embryos revealed the presence of severe lesions of a blood vascular nature in the head region, particularly in the region surrounding the eyes. The investigators associated the abnormalities of structure with these blood vascular extravasations which were common of the embryos and of the mice that died soon after birth. Bagg has, in previous experiments, shown that there is a strong tendency for blood vascular disturbances to appear in embryos subjected to irradiation.[1] While the investigators have no direct evidence that these two phenomena are related, they are inclined to believe the hereditary abnormalities described by Guyer and Smith are associated with early blood vascular lesions in the embryos.[2]

These eye defects which have shown themselves to be inherited are recessive in character and are apparently Mendelian in nature. On the other hand, of the two thousand carefully examined controls, not one displayed these eye defects.[3]

There is almost complete agreement that x-ray radiation of living tissue is associated with the production of deformed animals that often die shortly after birth. An outstanding characteristic of these irradiation experiments has been the ease with which eye defects have been produced. But it is evident, however, that x-rays have a modifying effect on the germ plasm, and therefore experiments with irradiation do not con-

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1-Bailey and Bagg, Effects of Irradiation on Fetal Development, Am. Jour. Obstet. and Gynec., Vol. 5, p. 133.
2-Bagg and Little, Hereditary Defects and X-Rays, Amer. Jour. Anat., Vol. 33, p. 136.
3-Little and Bagg, The Occurrence of Four Inheritable Morphological Variations, Jour. Exp. Zool., Vol. 41, pp. 45-91.

stitute a true test of the Lamarckian principle. The eyes of the x-rayed parents remained normal, and hence it cannot be said that an acquired eye defect was transmitted. Since most of the tests became sterile after the treatment, apparently the germ plasm had been altered, and the abnormal eyes represent the inheritance of a germinal modification and not the inheritance of a somatic change.

Although Bagg and Little undertook this experiment primarily to cast light on the work of Guyer and Smith (1918), it is not valid as a test of the transmission of an acquired somatic change.

PSYCHIC

McDougall's (1930) experiments with rats is so well known that a brief summary will suffice. He has tested up to his latest report twenty-three generations of rats to determine whether training is inherited. He used a tank of water having two gangways, one of which was lighted and the other dark. The rats were put into the tank and whenever they tried to escape by the lighted gangway, they received an electric shock. In time they learned to go to the dark gangway and to avoid the lighted one. McDougall claims that the number of errors have decreased up to the twenty-third generation, even when those rats that made the most errors were mated. Subsequent generations showed an inheritance of training. The experiment is being continued.

Agar, Drummond, and Tiegs (1935) have undertaken to repeat McDougall's experiment using the same general type of tank, with one gangway illuminated and the other dimmed, the lighted gangway being provided with an electric shock. They have taken pains to eliminate McDougall's greater errors. In the first place, only one rat was put into the tank at a time, whereas McDougall put several rats in at the same time. Thus the strong chance of one of the rat's behavior influencing the others was eliminated. Secondly, McDougall gave preliminary trials without shocks to determine the proclivity of the rat for or against the lighted gangway. Agar allowed no trials without shocks, thus eliminating a conditioning for or against

any gangway.

At the age of twenty-eight days training began, the light and shock being on the left gangway the first day, on the right gangway the second day, and so on alternately. Only four trials per day and a shock lasting only 1.2 seconds were allowed. From the sixth day on, there were six trials a day and a shock lasting three seconds. McDougall gives six trials per day and a full shock from the beginning. After the rat has learned, it is only given two trials daily till mating, except days when it makes an error, and is then given six trials. If it has not learned by the end of the fifty-second day of training (three hundred and two trials), it is given "special training" until it learns and is then given two trials daily. Training continues to the day of mating and never beyond. Two independent lines have been maintained for five generations and one for a sixth generation, each line being divided into parallel trained and control sub-lines, and tested against each other in sub-lines.

After six generations, the authors report, "No increase in facility of learning by the trained sublines as compared with the controls has ~~as~~ yet appeared."[1] The experiment is being continued.

Sonneborn (1931) points out that Professor Crew has found one serious flaw in McDougall's work, the possibility that the

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1-Agar, Drummond, and Tiegs, A First Report..., Jour. Exp. Biol., Vol. 12, p. 211.

trained parent rats communicated to their young something of the experience they have been through. Thus one would be dealing here not with genetical inheritance but "social" inheritance. And Professor Crew supports his criticism by an account of similar "social" inheritance among birds. To this criticism Sonneborn adds two more. In the first place, Sonneborn points out, it is possible that the "improvements" in learning in successive trained generations is an expression not of genetical differences but of differences in the strength of the electric shock used to time the rats.

The shocking apparatus was such that,according to McDougall, there was an unavoidable variation in the strength of the primary current, the behavior of the interrupter, and the kind of contact made by the rats.

The earlier generations were trained not by McDougall himself, but by an assistant, Mr. Heck. While the marked differences between the generations trained by Mr. Heck and those trained by McDougall may be due to genetic differences, it seems more probably that they were due to differences in the intensity of shocking. McDougall admitted his shocks varied from medium to heavy, while the existing data indicates that Mr. Heck's shocks varied from light to medium, thus casting serious doubt as to whether the differences can be considered as genetic.

Sonneborn's second criticism is that these same differences may have been brought about by "inadvertent selection."

McDougall found that there were differences in intelligence and that these differences were inherited. The selection, therefore, of the more apt would result in an increase in facility in the course of generations with no training at all.

The method used to prevent selection was to pick at random two individuals from each litter before training began; these animals were trained and bred and all litters born after training were equally represented in the selection made for training and breeding in the next generation.

Further, throughout the experiment all runts and obviously weakened animals were rejected. Then again, in the early generations at least, it seems that selection was not guarded against as closely as it was later "because McDougall obtained a new sample of rats for the purpose, as he himself says, of seeing what results would be obtained when special attention was given to the matter of selection. This new sample constituted his 'control' group. Thus the superiority of the later trained generations to the new 'control' stock might well be interpreted as due partly or largely to favorable selection for several generations in the one stock and the careful avoidance of favorable selection from the start in the other stock." [1]

Moreover, in the later generations (fourteenth to twenty-third) several facts indicate selection was not completely avoided. In each of these generations, as many as three rats

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1-Sonneborn, McDougall's Lamarckian Experiment, Amer. Nat., Vol. 65, p. 547.

were incapacitated from shock from further training and reproduction. On the basis of mere chance alone, it would seem that those eliminated were the worst ones. It is likely that those rats got the heaviest shocks which required more shocks in order to learn. Thus those eliminated by the fatal shocks were probably on the average the worse rats.

"Happily, each of these criticisms is susceptible of definite experimental tests. Only when these have been made can his very important conclusions be considered as fully borne out by his evidence."[1]

Vicari (1929) experimented with the mode of inheritance of behavior traits and maze learning abilities. Although she was not experimenting for the transmission of learning, she makes this observation. "From a study of three separate crosses involving around 900 mice through three and four generations of training, it seems clear that the later generations have not been aided in learning the maze by the training of their ancestors."[2]

MacDowell (1923) reports that he found no inheritance of the learning to run a maze of rats.

Sadovnika-Koltzova (1926) reports from her work on rats: "The teaching of parents does not influence the abilities of the offspring."[3]

1-Sonneborn, op. cit., p. 550.
2-Vicari, Mode of Inheritance . . . , Jour. Exp. Zool., Vol. 54, p. 82.
3-Sadovnika-Koltzova, Genetic Analysis . . . , Jour. Exp. Zool., Vol. 45, p. 318.

McDougall's (1930) experiments seem to offer good evidence for Lamarckism. But this work not only suffers from the flaws pointed out by Sonneborn (1931), but has been negated by the experiments of Agar, Drummond, and Tiegs(1935) who found no transfer of training in using the same technique, and by Vicari (1929), MacDowell (1923), and Sadovnika-Koltzova (1926) all of whom found no transmission of training. Pavlov, who claimed to have found the inheritance of conditioned reflexes, later retreated from this position, admitting that this sort of inheritance was complicated and uncertain, thus leaving the question open. Further McDougall's claim is a strain on any one's credibility. If there is such a thing as the inheritance of training, why does the offspring of the most erudite scholar have to learn from the very beginning? And why after centuries of learning does not the slightest evidence for an inheritance of knowledge exist among men? Experiments are showing conclusively that instincts are physiological reflexes and are not inherited as knowledge. If, for instance, a hen is castrated and testes are implanted, the hen will crow, strut about, taking over all the "sex instincts" of the male, thus demonstrating that instincts are not inherited as such, but only physiological structures are inherited.

PART IV

SUMMARY

THE EVIDENCE FOR AND AGAINST THE TRANSMISSION OF ACQUIRED CHARACTERS

It may be well, perhaps, to recapitulate the evidence for and against the transmission of acquired characters by drawing up a balance sheet.

What evidence can be put down as credit for the Lamarckian assumption? Kammerer's work with the midwife toad proves nothing but the effect of a selective environment upon developing organisms. And his work with the spotted salamanders is valueless because he did not carry enough generations to show indisputably that the modifications were permanently inherited. Sumner's work (1915) on temperature effects on white mice is also valueless since only one generation was carried.

Tower's (1917) experiments on the effects of a mesophytic environment on the beetle, L. decim-lineata, may be regarded as evidence for the Lamarckian assumption. However, the experiments lend themselves more readily to a selectionist explanation.

The polymorphic forms of the rotifer, g. Asplanchna, that were investigated by Powers (1912) do not show that inheritance of a somatic modification. Nor do the polymorphic forms of the rotifer Brachionus pala, which Whitney produced by using sodium silicate, constitute evidence for the transmission of

acquired characters. The modifications did not prove to be heritable.

Stockard and Papanicolaou (1918), MacDowell and Vicari (1921), and MacDowell (1927) found that the defects produced by alcohol were inherited. But the defects produced were germinal and not somatic.

The tendency to remain in chains and the inherited invaginated forms of Paramecia described by Jennings (1908) and Dawson (1926) may be taken as evidence for Lamarckism. However, it seems that these modifications were germinal rather than somatic.

The important experiments of Guyer and Smith (1918, 1920) have been rendered valueless by the failure of Finlay (1924) and of Huxley and Carr-Saunders (1924) to duplicate them. Furthermore, these experiments seem to have produced germinal modifications rather than somatic ones.

McDougall's work on the inheritance of learning in rats has been negated by the failure of Agar, Drummond, and Tiegs (1935), of MacDowell (1923), and of Sadovnika-Koltzova (1926) to find the slightest indication of an inheritance of training.

Thus only three experiments can possibly be regarded as evidence for the transmission of acquired characters. These three are the work of Tower, Jennings, and Dawson.

On the debit side of the balance sheet, we have the work of Castle and Phillips (1911) on ovarian transplantation. The mutilations of Colton (1931), Calkins (1911), Peebles (1912),

and Jennings (1908) are invalid since mutilations mean the dropping off of a character and not the acquiring of one. However, the fact that Colton found no inheritance of the highly developed hind legs of the biped rats remains as evidence against Lamarckism.

Northrop (1920), Zeleny (1928), and Krafka (1920) found no inheritance of temperature effects of Drosophila. Finesinger (1926) found no permanently inherited effects of chemicals on rotifers.

Pearl (1917) working with fowls, Noyes (1928) and Whitney (1912) working with rotifers, Hanson and Heys (1927) and Nice (1912) experimenting with rats, found no inherited effects of alcohol. But these experiments may be dismissed as evidence, since the effects of alcohol do not comprise a true somatic modification. The failure of Hanson and Heys, however, to find any inheritance of increased resistance to alcohol fumes stands as evidence against Lamarckism.

Donaldson and Meeser (1932) found no inherited increase of the musculature or body organs in the albino rat.

Hegner (1919) and Woodruff (1917) were not able to produce any heritable diversities in Paramecia.

Finlay (1924) and Huxley and Carr-Saunders (1924) were unable to corroborate the results of Guyer and Smith, although they used the same technique.

Lastly, Agar, Drummond, and Tiegs (1935), Vicari (1929), MacDowell (1923), and Sadovnika-Koltzova (1926) all report

negatively on the inheritance of training.

Thus, as evidence against the transmission of acquired characters, we have the work of Castle and Phillips, of Northrop, Zeleny, Krafka, of Hanson and Heys, of Donaldson and Meeser, of Finlay, of Huxley and Carr-Saunders, of Agar, Drummond and Tiegs, of Vicari, of MacDowell, and of Sadovnika-Koltzova.

CONCLUSION

The object of this paper has not been either to prove or to disprove the inheritance of acquired characters but to present the evidence for both sides and make an impartial estimate.

For practically a century biologists assumed that the Lamarckian theory was true, and much was taken for granted that could not be subjected to experimentation and verified thereby. There are those who shake their heads sagely and remark that they do not see how evolution could have been possible at all unless what has been acquired by one generation has been handed down to the next. But explanations, no matter how plausible, are not facts and are relevant only as tentative hypotheses for investigating the facts of the case. Again it must be remembered by Lamarckians themselves that interpretations are not facts. There are many adaptive characters in plants and animals which may be superficially interpreted as due to the results of use and disuse or of environmental influences. Uncritical minds prone to Lamarckism "see on modern flowers the footprints of insects ~~that~~ which have visited them for untold ages; they speak of the dwindlings of ~~a~~ the whale's hind-limbs through disuse, of the hardening of the ancestral horses' hoofs as they left the marshes and ran on harder ground; they picture the giraffe by persistent effort lengthening out its neck a few millimetres every century, as the acacia raised its leaves higher and higher off the ground; and they say that

animate nature is so full of evidences of the inheritance of acquired characters that no further argument is needed."[1] But this is begging the question. It is easy to find structures that may be inherited. It is easy to say the webbed feet of certain birds are due to walking in marshes, or the blind eyes of certain animals are due to living in dark caves. It is easy to say this but absolutely futile; it proves nothing.

Then, practically all the reputed cases of the inheritance of somatic modifications have either been disproven as such or have lent themselves to a more acceptable explanation. There have been so many carelessly claimed and unfounded "proofs" of the apparent inheritance of parental somatic modifications that we are justified in looking askance at such claims and in demanding precise techniques and methods. Nor have any group of experiments been large enough, nor conclusive enough to convince open-minded men interested in solving the modus operandi of evolution, and who are willing to accept the Lamarckian postulate when sufficient evidence has been presented.

Further, were somatic modifications the common course of evolution, should we not expect to find the process at work among us today or to have evinced itself during the centuries of recorded history? And should we not expect to find abundant positive experimental evidence instead of a few doubtful cases? Obviously the proof of the Lamarckian principle remains a mat-

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1-Newman, op. cit., p. 324.

ter of the future.

But let not the Weismannians think they have vanquished their Lamarckian foes entirely. Failure to prove the Lamarckian hypothesis does not establish the Weismannian theory as the full truth and nothing but the truth.

In the first place, it is common knowledge that the germ plasm is not impermeable to environmental influences. Many experimenters have succeeded in modifying the germ cells directly. Secondly, the Weismannian theory of germinal determiners fails to explain ontogeny. Microscopic examinations fail to reveal in the cells of a developing organism these determiners of Weismann. Even more disconcerting to the theory of germinal determiners is the phenomenon of regeneration whereby any undifferentiated cell may regenerate the lost part if placed in the proper position. Further Weismann was unable to explain polymorphism except by assuming alternate sets of determiners. As regards vestigial organs the Weismann theory breaks down entirely. Weismann himself recognized this and so invented the amusing theory of germinal selection or the "battle of the parts."

Nor does the circumstantial data from embryology, paleontology, and ecology lend itself to a germinal explanation. The germ plasm theory suggests nothing plausible as explanations for these phenomena and further, organic evolution is too complex to be determined by anything so simple as natural selection.

May it not be that the results of experiments fail to confirm Lamarck's belief because the proper conditions have not been reproduced? And may it not be that the weeks, months, and perhaps three or four years are far too brief to do what innumerable ages have done? The time element is a very just criticism of these experiments that disprove Lamarckism.

In closing, the suggestion is made that since the germ plasm is not impermeable to environmental influences, and since the Lamarckian principle has not yet been convincingly disproved, may not the truth lie somewhere between the two principles? One thing is certain, the discovery of the forces of evolution rests in the womb of the future.

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